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[1] Submitted for publication April 1946. The author is particularly obliged to various members of the Emergency Rubber Project, U. S. Forest Service, and of the Special Guayule Research Project of this Bureau for facilities, patience, and aid. Without the prompt and efficient help of C. B. Waldron in obtaining labor, equipment, and supplies, the field work would have been impossible. The drawings are the work of Juan Cardona, a Mexican national agricultural worker, whose services were offered by the Emergency Rubber Project. The constant advice and encouragement of A. C. Hildreth, Special Guayule Research Project, under whose direction this work was undertaken, have proved indispensable to its successful completion.

INTRODUCTION

The crucial need for rubber and the great interest in guayule (*Parthenium argentatum* A. Gray) as a source of this material gave impetus to extensive research on the nature, cultivation, and rubber yield of this plant. The agronomic investigations in particular revealed the need of a thorough survey of the root habits of the species. No better surroundings for such a root study could have been found than the sites of the many-faceted research to which guayule has been subjected recently near Salinas, Calif., and elsewhere in the Southwest. The ecological nature of the study has brought it repeatedly into contact with the investigations of the various agronomists, physiologists, soil technologists, and geneticists of the project. Many of the excavations on which this root study is based were performed in experimental plantings made by these men.

The principal purpose of this study was to furnish agronomists with information on root development that would serve as a biological basis for their explanations of plant behavior under various conditions involving root relations. Attention was given primarily to the responses of individual plants to the various factors of their habitats. Tillage, planting methods, irrigation schedules, fertilizer application, and yields received only passing notice, for they were being fully studied in the agronomic and soil research programs.

Before the discussion of the cultivated plant there are included the results of investigations of native guayule in the northern part of its range, namely trans-Pecos Texas. From reconnaissance associational analyses, detailed root investigations, and habitat analyses in a variety of localities there were gleaned a number of clues to the behavior of the species under cultivation. These results are kept separate in order to avoid confusing the study of cultivated guayule and to permit a more direct contribution to the ecology of the native plant.

The results presented constitute an autecological study of guayule from the standpoint of its root behavior. To accomplish this, observations have been concentrated on the ecological concepts of ecesis, adaptation, and competition. In any survey the indicated avenues for further research are apt to be fully as important as the positive facts revealed. Many problems are brought to light but only partially solved. Rather than permit these incomplete observations to be lost, some of them have been incorporated into the discussion as hypotheses.

No previous root studies have been made specifically on guayule beyond the pioneer observations by Lloyd (*11*)[2] on native plants in Mexico and brief mention of the root habit of cultivated ones by Artschwager (*1*). The present investigations bore out the results of these authors in most respects so far as the earlier studies proceeded. The studies of other investigators (notably Weaver and his associates) on other species, both native and cultivated, are the basis of the present knowledge of root habits, development, and ecological relations. These are referred to as the specific points are taken up. Among biological subjects root habit of a given species is unique in being so definite that difference of opinion between investigators is rare or nonexistent.

[2] Italic numbers in parentheses refer to Literature Cited, p. 114.

MATERIALS AND METHODS

Field investigations of roots were made by the "bisect-wash" method of Tharp and Muller (*16*). This consists of sinking a trench immediately in front of the plant to be studied to a depth calculated to exceed the greatest root penetration. The vertically cut surface is smoothed to a uniform plane in front of the axis of the plant, and cords are stretched vertically and horizontally on this plane to serve as guides in studying and drawing. The soil is gently washed from the roots by means of a fine jet of water supplied by a tank under 60 to 120 pounds of pressure. The force of this jet is manipulated to suit the need by adjusting a valve at the nozzle.

The washing is begun at the top and proceeds downward, an effort being made to remove soil to a relatively uniform thickness. The roots thus exposed constitute a thin bisection of the cylinder which is the root system. As the washing progresses, even if two men are excavating, there is ample time for an artist to record in a drawing each root as it appears and any breakage can be noted as it occurs.

The bisect-wash method is very rapid and should be highly accurate. Care in washing and drawing and practice on the part of the excavator to develop a sense of comparable sampling will eliminate most of the errors. Two standards of sample volumes were employed in this study. In the case of seedlings and small plants the root systems were revealed in their entirety. Larger plants were sampled by bisections 6 inches in thickness. The temptation to follow a root that passes beyond the scope of the bisection is often very great, but to do so reduces the accuracy of the sample.

The rapidity of the method of excavation is revealed in the great number of investigations completed. In a period of slightly less than a year, actual field time, 87 pits of all sizes were dug. In these the root systems of 1,375 plants were excavated, studied, and illustrated by a crew consisting of 1 or 2 excavators, 1 artist, and occasionally 1 laborer.

The choice of individual plants to serve as a sample of any given planting is always a problem. The number of observations was not great enough to permit replication and randomization of samples, a procedure that would have made the study long to the point of impossibility. Random sampling, of course, is the only method that excludes entirely the personal element. The use of such methods to choose a single site to represent thousands of plants was unsuited to this study for several reasons. The danger of hitting upon a genetic weakling, a diseased specimen, an ecologically poorly adjusted plant, or some other oddment equally unrepresentative is too great to permit random methods. In order to standardize the competitive factor, samples were selected only in perfect stands. Choice was resorted to, and an effort was made to include (1) no plants showing obvious abnormalities, (2) only perfect stands, (3) no plants among either the smallest or the largest size classes in the field, and (4) no guard rows. As the study progressed to abnormalities, of course, these prohibitions were relaxed individually. The fact that degree of normality of root development is in most cases faithfully reflected by aerial plant development made the choice of representative samples of older plantings quite easy.

In general, no evidence was encountered of any appreciably great variation in root development independent of top development in mature plants. An exception to this occurs rarely as a result of soil variations that might not necessarily affect top growth, and a special study of this phenomenon was made. Also, in very young plants this relation was found not to hold. Obvious genetic abnormalities were avoided, and the homogeneity of the samples is evidence that relative genetic similarity was obtained.

Lack of time and the requirement of care not to damage the experimental plantings limited the size and location of excavations. Samples ranged in size from 2 to 6 plants in older plantings and from about 20 to over 100 in the case of small seedlings. In retrospect these ranges in sample size have proved sufficient in that no great variations appeared within samples or among those of similar plantings.

The field studies were designed to investigate the effects of age, cultural methods, competition, soil variations, and moisture supply on root habit. Chronologic studies of root development in both seedlings and transplants, analyses of root development under various degrees and kinds of competition and irrigation, and a study of the effects of every available soil type were carried out. In the study of soils attention was paid not only to the general root physiognomy of plants grown in a given soil type but also to the details of growth responses to vertical soil variation.

With few exceptions, the cultivated guayule studied was of the strain 593 selected by the Intercontinental Rubber Co. early in its research program. These exceptions were of strain 406, a selection similar to 593. Studies of native guayule involved the natural stands of the species in trans-Pecos Texas.

GENERAL CHARACTER OF GUAYULE

Lloyd (*11*) described guayule in detail, and only a few points pertinent to its ecology need be mentioned here. The species is a single-stemmed shrub reaching 2 or 3 feet in height. It branches near the ground level, a condition that gives it a broad bushy appearance; the usually even distribution of twigs results in a rounded crown. The roots form a modified taproot system. In early stages the taproot habit is obvious, but successive production of laterals soon obscures the primary root and the mature system is fibrous in appearance.

Most crops are distinctly mesic in origin, but guayule is unique as a crop plant in having many of the attributes of a desert species. However, it cannot be classed as a true desert one, even though its range in trans-Pecos Texas and north-central Mexico lies entirely within the desert region. Its altitudinal range is restricted to a narrow transitional zone lying between desert and grassland elevations. Its response to cultivation clearly indicates a high tolerance of soils and moisture conditions of neighboring grassland areas, and it apparently is restricted from the less xeric sites principally by competition. In fact, the species is characterized by very poor competitive ability, a condition that in the wild gives it the appearance of a species with very narrow tolerances. Actually, exclusive of competition and extremely xeric conditions, its tolerances are exceedingly wide, as demonstrated in this bulletin.

Among the xerophytic characteristics of guayule are the possession of a heavy indumentum of trichomes, the faculty of shedding most of its leaves and becoming dormant in time of drought, and the ability to respond rather quickly to new supplies of moisture by prompt water absorption and leaf production. The species has been observed to survive long periods of severe drought, high temperatures, and high evaporation in a state of apparent inactivity, when its root system nowhere reached moist soil. This characteristic would place guayule in the class described by Shantz (*14*) as "drought enduring." The drought-enduring habit is shown rather early in the life of the plant, seedlings only 6 months old surviving severe droughts of 3 months' duration or more. However, such ability to survive is no indication of its success as a desert plant. Under truly desert conditions the seedlings fail of ecesis, apparently because their vigor of growth under low-moisture conditions and their toleration of protracted drought periods are not so great as those of genuine desert species.

Although no specific data are available, it is obvious from the observation of cultivated guayule as well as of the native shrub that fairly large amounts of water are required for its most active growth. The species goes into a dormant condition while associated plants of other species with similar root depths are still quite active. Thus, although guayule is drought enduring to a remarkable extent, its water requirements during its periods of activity are distinctly mesophytic.

Guayule is also somewhat tolerant of water. Inundation for a few hours and very moist soil of both light and heavy texture had no ill effect in many cases. However, high moisture at some temperatures, particularly in the presence of certain parasites, often results in fatal infection or drowning. High mortality from root and crown rots often follows excessive irrigation (*2*).

The character of guayule, then, is that of a semidesert species, and as such its responses to culture are in many respects dissimilar to those of most crops. Although its xerophytic characters increase its tolerance of moisture depletion, it will be seen that relatively mesic conditions are required for its economic production.

ECOLOGY OF NATIVE GUAYULE AND MARIOLA

The ecology of native guayule consists of its development in its native range, its relations to the physical factors of its environment, and its interrelations with the biotic influences of its habitat. The fact that ideal cultivation is the very antithesis of the conditions under which guayule grows naturally makes the study of native guayule exceptionally valuable in interpreting phenomena of cultivation. Influences which cause certain undesirable growth responses in cultivated guayule are found in much more extreme form in the wild, and their effects are more easily and more certainly ascertained there.

Habitat of Native Guayule

Guayule occurs naturally in a region comprising the northern and eastern three-fourths of the Central Plateau or Chihuahuan Desert in Mexico, parts of northeastern Coahuila, and about the southern half of trans-Pecos Texas. It by no means occurs in all parts of this region. Vast stretches of the Chihuahuan Desert are too hot and dry for its growth, and much of the country does not harbor the species. Within the general range, its distribution is limited to a narrow altitudinal range varying with latitude and to an even more precise topographic range. Its altitudinal limits range from 2,300 to 3,500 feet in the northern and northeastern extremes of its range in Reeves, Pecos, and Terrell Counties, Tex. In the Big Bend in Presidio and Brewster Counties, Tex., it ranges from 3,500 to 4,200 feet. Lloyd (*11, p. 14*) reported the species reaching elevations in excess of 7,000 feet in Mexico. Indeed, most of the guayule observed by the present author in Coahuila occurred above 5,000 feet. As one progresses into the more rigorously desert parts of the region, correspondingly greater elevation is required for the development of the specific climate to which native guayule is restricted.

The climatic tolerances of guayule are actually very wide when viewed from the standpoint of its growth in various localities. Its persistence in the wild in districts of Texas where temperatures of −7° F. have been recorded, its tolerance of exceedingly hot and dry summer periods over most of its range, and its luxuriant development under irrigation equal to heavy rainfall cover a very wide range of conditions. Yet, in native stands the species is restricted to a series of narrow bands corresponding roughly to the xeric lower limits of grassland climate. These climatic zones are locally induced by elevation. Unfortunately there are few meteorological observatories located near the sites of native guayule stands. Estimates based upon the rainfall values credited to these and adjacent localities and the distribution of native vegetation would place the average annual rainfall of the guayule country of trans-Pecos Texas between 12 and 14 inches. This falls principally in late summer and early autumn with an occasional second minor wet season in late spring. Although there is no season characteristically without rain, droughts of great length and intensity may occur and often do.

The restriction of guayule to a narrow band transitional between desert shrub and grassland is the result of two limiting factors. The lower limit of guayule distribution is probably fixed by low rainfall and corresponding rigorous desert conditions in which guayule cannot grow. The upper limit is determined by severity of competition offered by grassland species.

In addition to the transitional climatic type in which the moisture requirements of guayule are met and those of competing species are less fully met, another environmental influence favors guayule. This is a topographic character usually encountered where the species is found. Where the climatic conditions are very favorable, such as on Bandera Mesa, Presidio County, and on the gently rolling hills of the 02 Ranch country, south of Chalk Draw, Brewster County, guayule may develop very well without the aid of any specific topographic feature. Its best development, however, occurs on the slopes of foothills where the thin, rocky soil is less favorable for grassland species and a high percentage of runoff limits depth of water penetration and thus favors guayule over deep-rooted desert shrubs. Such topography sometimes carries the plant to elevations in excess of its usual range. However, topography alone is by no means sufficient to account for the distribution of guayule. Many very favorable slopes devoid of guayule occur at elevations too low to induce the requisite climate, and such areas bear only desert shrubs.

Lloyd (*11, pp. 20, 23–25*) speculated variously that guayule is restricted from level alluvial soils by their acidity, humus content, and poor aeration and favored by the superior water-holding capacity of the soil of the foot slope. Recent successful germination and cultivation of guayule in soils of acid reaction and of high humus content eliminate those two factors. Poor aeration may locally inhibit guayule, but much of the flat country consists of adequately aerated soils bearing no guayule. Actually, the water-holding capacity of the foot slope is inferior to that of the plain. The conclusion is inescapable that the dense growth of grasses and shrubs on the alluvial soils of the plains of greater elevations is responsible for the failure of guayule to grow there. Its poor competitive ability does not permit it to grow in the more favorable soils even if the climate is ideal for its growth. The plains of lower altitude, and even the lower foot slopes and foothills, afford a climate too rigorously xeric for guayule.

One universally present condition of the habitat of native guayule is a calcareous soil. Limestone or shale substrata usually accompany the species, but on Bandera Mesa and near Shafter, Presidio County, occur two stands independent of a lime substratum. The parent rock in both cases is an igneous intrusive once overlain by Upper Cretaceous limestone and shale (*13*), but these have been eroded away and persist only here and there at these localities. However, the weathering of the superimposed lime resulted in considerable leaching of calcium into the underlying igneous material. Particularly as the igneous rock began to weather, the remaining calcareous remnants were incorporated in the thin, stony soil. Igneous stones partially buried in this soil bear a heavy accretion of calcium carbonate over those parts of their surfaces in contact with the soil. The presence of lime in the soil is enough to serve the needs of the guayule. A highly calcareous soil is not required for growth of the plant, for plantings of guayule on acid soils of granitic origin grow very well. However, no natural occurrence of guayule in a soil of acid reaction has ever been recorded.

In summary, guayule grows naturally on calcareous hills at elevations having a climate corresponding to the transition from desert to grassland in a region centering in the northeastern part of the Chihuahuan Desert. However, there are millions of acres of limestone slopes of the proper elevation and climate within this region on which no guayule now occurs and on which it is not known ever to have grown. The local distribution of the species is sporadic and entirely without apparent reason. Although disturbance involving both browsing by animals and exploitation by man has made great inroads on the native stands, it has never resulted in the extinction of stands except where the plant had had only a precarious tenancy. Vast areas in Mexico that had never been exploited and had not been developed for ranching showed this same character of sporadic occurrence of guayule. Lloyd (*11*) gave the impression that such irregular distribution did not occur in the region of greatest density of guayule, namely Zacatecas and neighboring areas.

The details of the characteristics of individual sites are presented in the discussion of the root studies and associational analyses.

Root Habit of Native Guayule

The semidesert habitat in which guayule grows naturally is characterized by extreme unbalance. Aerial space and soil surface are ordinarily never fully utilized and light is intense, but soil depth is limited and available moisture is entirely lacking during much of the year. The factors that limit growth, then, are those of the soil; the most significant relations between the plant and its habitat are to be found in the roots.

ROOT SYSTEMS OF MATURE PLANTS

The relations of guayule to its native habitat are best seen in the pattern of the mature root system. This reflects the very rigorous habitat faithfully. Since the sites of guayule are fairly constant in their shallow soil and shallow water penetration, the root pattern also is fairly constant. Undoubtedly some exceptions exist, but none were encountered in this study in which five mature plants and numerous seedlings and intermediates were excavated.

The native shrub permitted to develop free of heavy competition produces a very symmetrical and dense fibrous root system. The original taproot loses its prominence in the maze of laterals and their branches, but quite large plants may still show taproot dominance, especially in deeper soils. Lloyd (*11, p. 50*) failed to note this suppression of the taproot. Total depth of penetration is strictly determined by the depths of penetrable soil and of wetting resulting from the limited rainfall and heavy runoff. Lateral spread is limited only by the size of the plant, the availability of favorable soil to the extended roots, and the proximity of competing individuals. The greatest concentration of feeder roots is in the upper 6 inches of soil, effective soil occupation extending within an inch of the surface. Whereas cultivated plants are characterized by root systems much deeper than broad, those of native plants are quite the opposite, being twice or several times as broad as deep.

Intensive root studies were made in the guayule stands south of Chalk Draw in the 02 Ranch country about 50 miles south of Alpine, Brewster County, Tex. The rolling hills of this locality are composed of Boquillas flags (*13*), limestone flags ranging in thickness from an inch upward, alternating with beds of yellow clay or shale. The soil, insofar as it has developed in this rough terrain, is Ector stony loam. Near the surface the flags are broken into small pieces averaging about 8 inches in diameter, while at the surface occur fragments the size of coarse gravel. Infiltrating the cracks and spaces between the limestone fragments is a fine loamy soil fairly rich in humus. At a depth of 9 to 14 inches this is underlain by a bed of soft, amorphous caliche 8 to 21 inches in thickness. Beneath this, dry shale and unbroken limestone flags alternate. The surface soil, about a foot in thickness, is very pervious to moisture and roots, but the limestone inclusions occupy about 75 percent of its volume. The soft caliche layer is slightly penetrable by roots, cracks and old root channels being responsible for nearly all of the penetration by guayule roots. Its surface is very hard, being encrusted with consolidated materials resembling calcite.

At the time of the excavations (about the middle of May 1944) the entire soil profile was below the wilting percentage of moisture content, being powder-dry and dusty. All the guayule in the surrounding area was fully dormant and had shed the greater part of its foliage. General moisture penetration was judged to be about 2 feet, but a thin layer of moist shale was observed overlying an extensive sheet of thick limestone at a depth of 4 feet. Here, however, there were no guayule roots and only one heavy woody root of an unidentified species among the neighboring shrubs. It is likely that unusually deep water penetration occurs locally through fissures, and the substratum is said to be so pervious that all attempts to locate water at reasonable depths have failed.

In figure 1 is illustrated a plant growing in a site with 13 inches of sur-

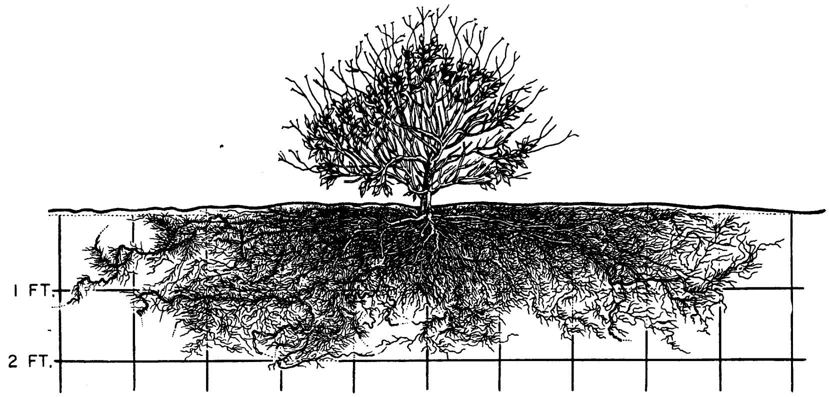

FIGURE 1.—Native guayule about 30 years old in Ector stony loam in Brewster County, Tex.

face soil underlain by 8 inches of caliche over a bed of shale. In this plant the most dense concentration of feeders occurred in the surface 3 inches of soil. Note the very crooked courses of the numerous principal roots caused by their turning in and out among the flagstones and, in the second foot, following the irregular leads of cracks and old root channels in the caliche layer. A few roots passed the lower limit of the caliche, but in the rarely moistened shale bed they either stopped or turned to one side. On the basis of ring counts, this plant (fig. 1) was estimated to be about 30 years old. Although it was subjected to considerable competition, it was less affected than most individuals in this locality. The protracted drought to which it was being subjected at the time was causing some loss of roots, especially among the dense, fine feeders of the surface inch of soil. An occasional principal root up to 2 mm. in diameter was found to be dead near the extremities of lateral spread. Such losses were assumed to have been caused by drought, but they might have been the result of age and excessive crowding and effected by a mechanism of self-pruning.

GROWTH AND DEVELOPMENT

Native guayule seedlings develop in much the same manner as those under cultivation. They differ only in that they experience very short periods of growth interspersed with long ones of drought dormancy. In the 02 Ranch locality near the plant shown in figure 1 were encountered many seedlings that apparently had germinated during the late-summer and early-fall wet season of 1943 and were probably 7 or 8 months old. Histological examination proved them to be less than a year old, and there had been insufficient moisture during the early spring of 1944 to produce any verdure at all. A few of these seedlings studied May 8, 1944, are illustrated in figure 2. Their root and top development corresponds roughly to that of 19-day-old cultivated seedlings. (See fig. 21, p. 31.) They apparently had had only 3 or 4 weeks of favorable moisture before either depletion of moisture or advent of low temperatures stopped their growth. When they were studied in May 1944, there was no evidence of available moisture in the soil. Their roots had suberized, but no necrosis was noted. A few of the smallest plants had died of drought.

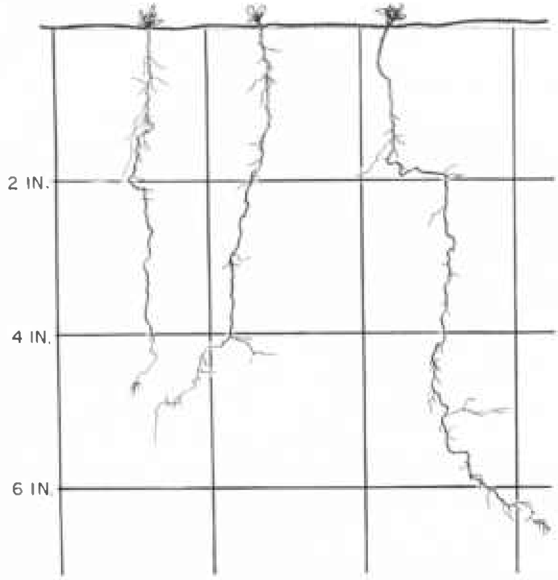

FIGURE 2.—Native guayule seedlings 7 or 8 months old surviving in powder-dry Ector stony loam near the plant shown in figure 1.

On October 20, 1944, after the late-summer rains, these seedlings were observed again. In figure 3 is shown the remainder of the population from which the plants of figure 2 were taken. Their much advanced top development as compared with that of the younger plants is evident.

FIGURE 3.—Native guayule seedlings of the same population as those shown in figure 2. They were about 1 year old when photographed, after the late-summer rains.

Topography and the nature of the soil surface play an important part in the incidence of seedlings. Slopes subject to sheet erosion and therefore very rocky showed no seedlings in 1944. Minor level spots on such slopes where small catchments of soil occurred, on the other hand, occasionally harbored a few seedlings. Hilltops and gentle slopes with a fair soil mantle were generously sprinkled with seedlings. Rocky sites, no matter how level, bore none. A small amount of duff was not detrimental to germination, but thick layers excluded the seeds from contact with the soil and effectively prevented germination.

Second to soil, the presence of a nurse plant seemed most effective in inducing seedling persistence. On favorable soil almost every plant capable of casting a shade was sheltering a few to many seedlings. Where seeds were abundantly scattered, not only guayule but various other species served to protect guayule seedlings by reducing insolation and evaporation. However, the most favorable soil areas bore abundant seedlings quite independently of nurse plants.

Additional root excavations were made in another locality about 17 miles east of Balmorhea, Reeves County, Tex., on the north slope of a small butte just east of Barilla Creek. The butte is composed of horizontal layers of thick limestone alternating with beds of shale and clay comprising Upper Cretaceous deposits (*13*). The soil is Ector gravelly loam with a subsoil of shaly clay. Large fragments of limestone make up about 20 percent of the gray friable clay loam surface soil. Below 18 inches there is a friable weathered clay mottled gray and yellow. Below 30 inches the clay shows little evidence of weathering and probably is very infrequently reached by moisture. This depth corresponds to the maximum penetration of guayule roots in this locality, but certain associated shrub species are obviously deeper rooted. At the time of the study the entire profile was strikingly dry, and the guayule was completely dormant.

A representative small population of guayule of various ages (estimated from a study of growth rings) is shown in figure 4. The taproot

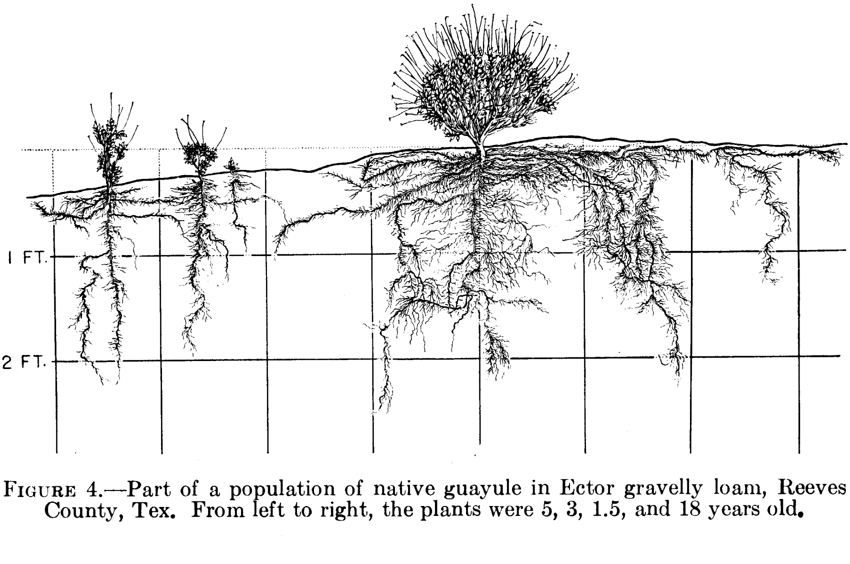

FIGURE 4.—Part of a population of native guayule in Ector gravelly loam, Reeves County, Tex. From left to right, the plants were 5, 3, 1.5, and 18 years old.

habit was maintained for a long period and was still discernible even in the oldest plant in which the laterals had assumed dominance. In figure 5 another plant adjacent to these is illustrated. Its age was estimated as 15 years. Here, too, the taproot habit was still visible as a relic, but the heavy fibrous development of the lateral system was well under way.

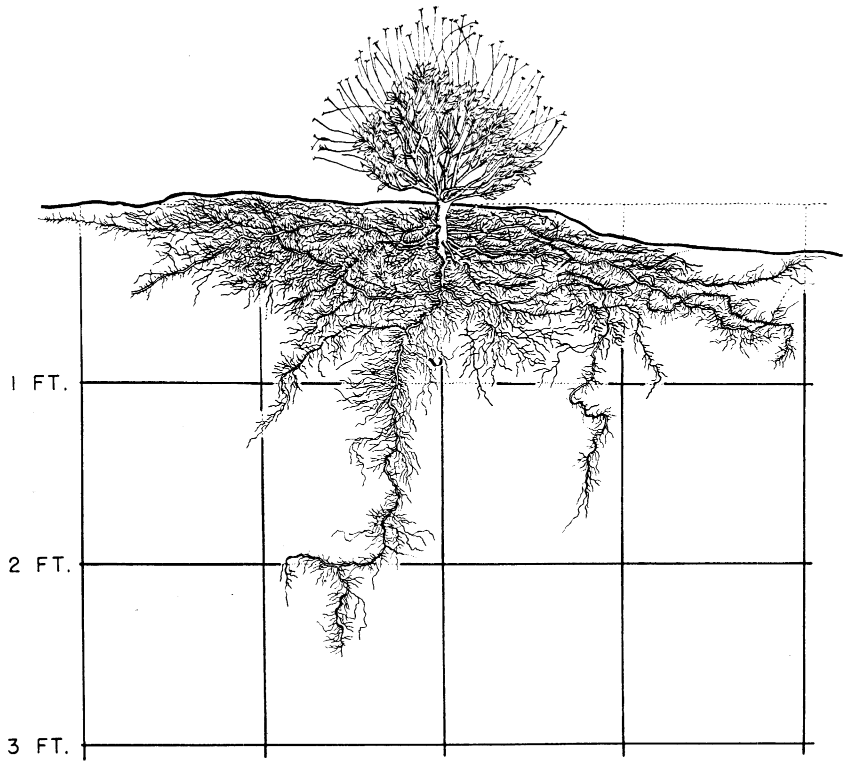

FIGURE 5.—Native guayule about 15 years old—a part of the population shown in figure 4.

As in the 02 Ranch locality, some dying of the finer and most extended feeders was observed on the older plants. It was most noticeable in the surface inch of soil and probably resulted entirely from drought. The lower limit of root penetration was undoubtedly set by moisture, for the clay subsoil was so fractured that root penetration should have been easy. However, the weathered upper 12 inches of the clay had a high water-holding capacity, its moisture equivalent being 22 percent. To moisten this layer and permit still deeper percolation would require a greater precipitation than the average annual rate of 14 inches characteristic of this region, especially on a slope so favorable to runoff.

REPRODUCTION BY ROOT SPROUTS, OR RETOÑOS

A relatively important phase in the life cycle of native guayule is the habit of root sprouting. This method of reproduction plays an important role in the persistence of the species on the thin-soiled, rocky slopes it most commonly inhabits. Whether the sprout issues from an exposed root still attached to the mother plant or from the exposed end of a broken root surviving the destruction of the parent, it is capable of developing and augmenting the population. Such an offset is termed "retoño" by the Mexicans. The word was adopted by Lloyd (*11, p. 61*) for both types of root sprouts, the residual root sprout being called an "induced retoño" and the sprout from the attached root a "natural retoño." After harvest of native shrub the incidence of induced retoños is relatively high, especially if the harvesting period is followed by effective precipitation. In the 02 Ranch locality the shrub was harvested during the winter of 1943–44. When examined about the middle of May 1944, a few of the exposed roots had sprouted weakly (fig. 6). Be-

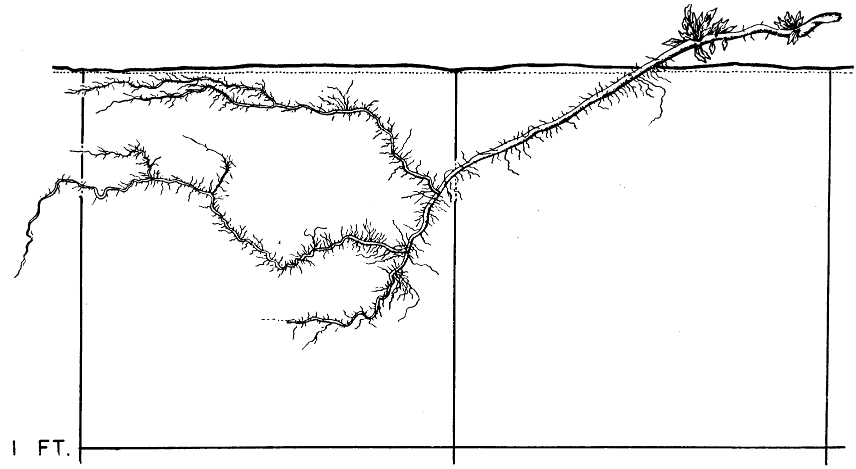

FIGURE 6.—Root sprouts of native guayule in Ector stony loam in Brewster County, Tex., from a residual lateral root exposed by harvest of the parent plant the previous winter.

cause of the failure of winter and spring rains, the vast majority were not active but the roots were still alive. Upon reexamination of these on October 20, 1944, after effective late-summer precipitation, almost all the exposed root stumps had sprouted after about 9 months of inactivity. Some of those recognized as having resumed growth the previous spring were by that time quite advanced.

Natural retoños are the more important sort occurring in native stands of guayule. As was pointed out earlier, rocky slopes lacking in soil produce few or no seedlings. On just such slopes natural retoños are apt to be very common, for erosion often uncovers the shallow lateral roots and leaves them exposed and subject to bruising by rolling stones and the hoofs of passing animals. Bruised cortical tissue seems highly disposed to produce adventitious leaf buds.

In figure 7 is illustrated an 11-year-old plant bearing two retoños in the Balmorhea locality. The stem tissue of the retoños revealed them to be less than a year old when they were encountered on May 2, 1944. The parent root had been completely exposed by erosion of the soil. The swelling of the parent root at the place of sprouting is characteristic and is followed by eventual atrophy of the root above the retoño. The

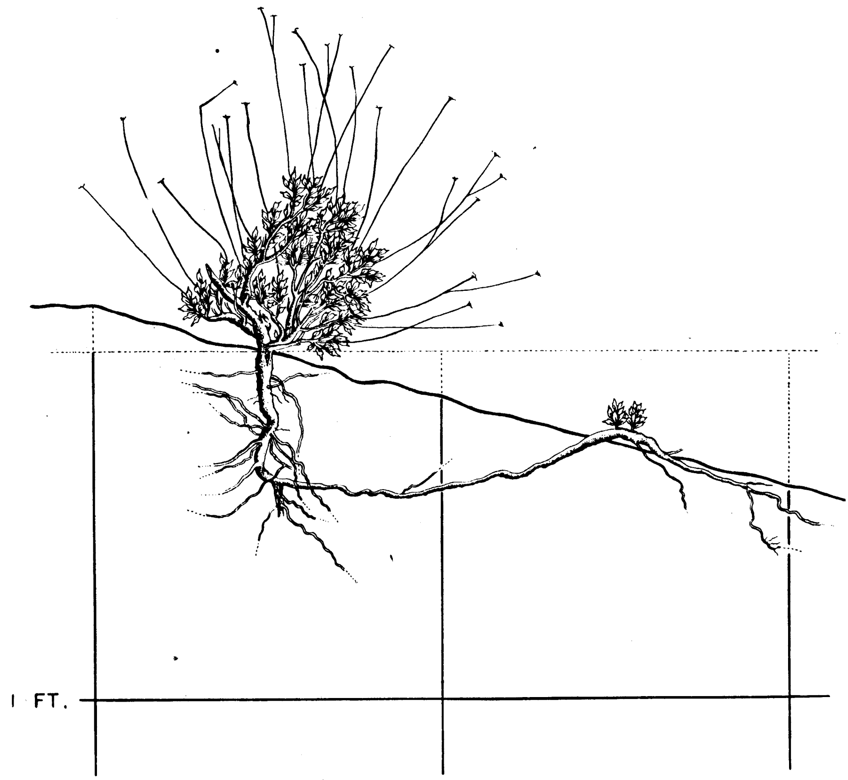

FIGURE 7.—Retoños less than 1 year old from the exposed lateral root of an 11-year-old native guayule plant in Ector gravelly loam in Reeves County, Tex.

swelling probably results from the increased food supply furnished by the photosynthetic activity of the retoño.

In figure 8 is shown a 20-year-old plant bearing many-stemmed retoños 6 or 7 years old. Note the large area of scar tissue on the exposed root at the base of the retoños.

Retoños are more apt to survive the hazardous early years than are seedlings, for they have the advantage of partially developed root systems inherited at the outset from the parent plant. The comparative rarity of retoños, especially on good soil, makes this means of reproduction assume strictly secondary importance except on very rocky slopes.

HABITAT AND ROOT HABIT OF NATIVE MARIOLA

As the closest relative of guayule and its omnipresent competitor in the wild, mariola (*Parthenium incanum* H. B. K.) merits attention. Mariola is one of the most fully lignified species in the genus, and guayule is somewhat less so. Its distribution differs from that of guayule in being considerably wider in both geographic spread and altitudinal range. Both its tolerance of desert conditions and its competitive ability permit it to invade simultaneously the desert-shrub zones of the lowland and the grassland of upper elevations. In addition to occupying practically

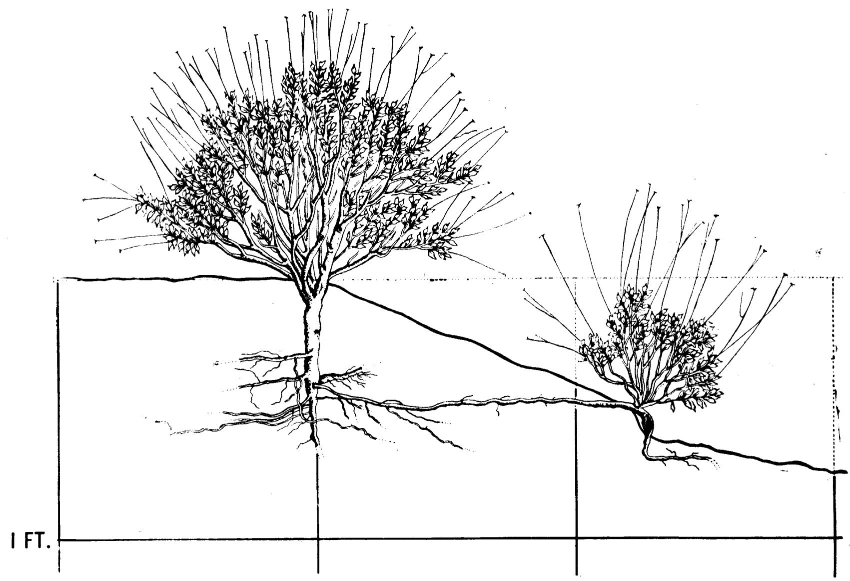

FIGURE 8.—Retoños about 6 or 7 years old from a 20-year-old parent plant of guayule at the site of those shown in figure 7.

the whole of the geographic range credited to guayule, mariola is found to the west in Sonora, to the east in Tamaulipas and in southwestern Texas, and to the north in New Mexico and Arizona, well beyond the known limits of native guayule.

Although mariola contains a small quantity of rubber, its yield is so little as to be wholly uneconomical as a source of this material. The species has often been confused with guayule by untrained observers; as a consequence, early surveys, especially in trans-Pecos Texas, were frequently overly optimistic and resulted in outlays of capital out of all proportion to the actual supply of guayule to be exploited.

The characters of mariola that permit it to grow beyond the limits of guayule are fundamentally physiological, and they cannot be related to any observed morphological features except in a secondary way. Greater tolerance of extreme drought and low temperatures and more vigorous competitive ability seem to comprise its advantages in invading any given site. The persistence of the individual on a certain site is aided by the habit of the plant rather than by the longevity of its tissues. Although guayule stems upward of 40 years old are not uncommon, the oldest mariola stem studied was only 12 years old. Yet, the short-lived mariola persists more successfully than guayule by means of its vegetative reproduction. Whereas guayule reproduces vegetatively rather uncertainly by means of retoños at some distance from the parent plant or by retoños from residual roots upon the death of the parent, mariola produces tillers at a rapid rate while the parent plant is still quite young. These offsets are grouped around the base of the stem and therefore effectively hold the site when the short life of the parent stem has run out. This habit was described by Lloyd (*11, p. 53*), but he did not note its survival value.

The tillers of mariola arise as leafy buds at the surface of the soil. As such a bud grows into a shoot, it strikes roots from its heel and is independent at an early age although still organically connected with the parent. Upon the death of the parent, the several offsets, then no longer connected, remain intertwined to form a colony which functions as an individual. By this time the older offsets have already begun tillering, and so the process continues. The resulting individual is a true bush and quite unlike the single-stemmed guayule shrub. The bush habit is shared by many of the species of the desert-shrub zones, and these are very abundant in the transition zone occupied by guayule.

The root system of mariola is not appreciably different from that of guayule; the differences alluded to by Lloyd (*11, pp. 20, 53*) were not found. The colony of individuals comprising the bush produces a composite root system whose physiognomy is very similar to the organically connected system of the single-stemmed guayule shrub. In figure 9 are

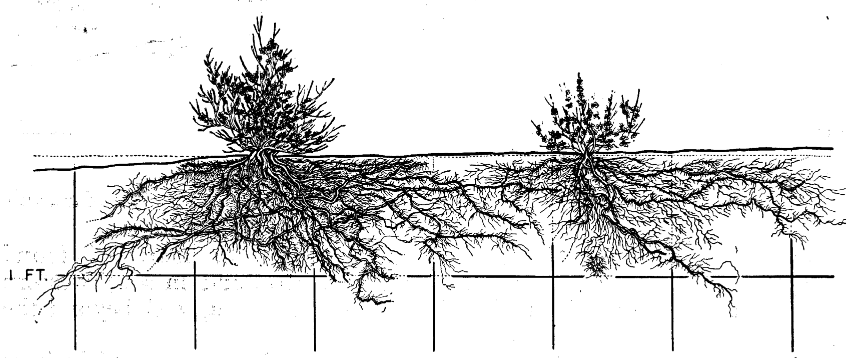

FIGURE 9.—Native mariola in Ector stony loam (immediately adjacent to the site of the guayule plants shown in figure 11) in Brewster County, Tex. The several principal stems (tillers) of the plant on the left were 6, 9, 9, 9, and 11 years old. The larger plant had already lost its older stems, but the smaller still retained the original shoot, which was 7 or 8 years old. Both plants were still producing tillers abundantly.

illustrated two mariola bushes from the 02 Ranch locality. (Compare these with the 20-year-old guayule adjacent to which the mariola grew; see fig. 11.) Aside from the somewhat shallower penetration and more limited lateral spread of mariola, there is no great difference. The plant on the left in figure 9 was nearly mature; the original parent and one offset had died. Of the remaining stems, the larger were 6, 9, 9, 9, and 11 years old, respectively, and were actively producing tillers. The plant on the right consisted of a single original seedling 7 or 8 years old and several small offsets still attached. Its root development was very poor to the left where the older plant held the advantage of prior occupation.

SOCIOLOGICAL RELATIONS OF NATIVE GUAYULE

Since sociological phenomena are so intimately related to the autecology of each species involved, it is not possible to separate entirely the two subjects. Part of the autecology of guayule has been discussed previously; additional points, as well as some relating to other species, must be used as the basis of an analysis of the social relations of guayule.

BIOTIC COMMUNITIES

The plant-animal associations in which guayule occurs have never been subjected to complete analysis and classification. To do so would be a huge undertaking involving hundreds of analyses in surrounding and related communities. This task was only begun and the sketchy results will serve only to orient the present study.

It has been pointed out previously that guayule is restricted to a transitional belt lying between grassland and desert shrub. The ecotone between these two formations is a relatively broad and fluctuating one, and as such it has been variously interpreted by early and recent workers. Only a few associations in the heterogeneous ecotone are hospitable to guayule, and therefore a consideration of the ecotone as a whole is superfluous to the present needs.

The desert subtending the lower altitudinal limits of the range of guayule was described by Shreve (*15*) as Chihuahuan Desert, a usage in which he followed earlier workers, including Lloyd (*11*). It is characterized by dominance of *Larrea tridentata* (DC.) Cov. over a wide area and more restricted dominance of *Flourensia cernua* DC., *Prosopis velutina* Woot., and various other low shrubs. In the northern part of the region, especially on limestone hills, a succulent phase of the desert shrub is developed. Here the regional dominants just mentioned form characteristic communities only locally on sites of well-developed soil and level topography. The more generally distributed "rough stony" land of the limestone and igneous hills and detrital fans is characterized by a strong concentration of leaf- and stem-succulents, such as *Agave lecheguilla* Torr., *Euphorbia antisyphilitica* Zucc., *Jatropha dioica* Sessé, *Opuntia leptocaulis* DC., *O. imbricata* (Haw.) DC., *O. macrocentra* Engelm., *Echinocereus* spp., *Ferocactus* spp., *Hechtia* sp., *Dasylirion leiophyllum* Engelm., and *Yucca baccata* Torr., mixed with *Larrea, Flourensia,* and *Prosopis*. The abundance of *Fouquieria splendens* Engelm. in this area is also characteristic. It is the succulent desert shrub whose upper altitudinal limits harbor guayule in the northern sector of the species' range. Next above the desert-shrub formation with its many associations occurs the variable and unstable desert-grassland transition occupying a broad belt of heterogeneous habitats basally subtending true grassland.

Grassland proper in southern trans-Pecos Texas is confined to elevations of about 5,000 feet or more with rainfall in excess of 14 inches annually. The greatest single area of such country centers about the igneous Davis Mountains. The development of true grassland on limestone substrata requires slightly greater elevation and higher precipitation. The grassland of trans-Pecos Texas is dominated by short-grass species including *Bouteloua hirsuta* Lag., *B. gracilis* (H. B. K.) Lag., *B. curtipendula* (Michx.) Torr., *Buchloë dactyloides* (Nutt.) Engelm., and *Aristida* spp. in various combinations. Bunch grasses such as *Andropogon saccharoides* Swartz and *A. scoparius* Michx. occur only locally on the most favorable sites. Forbs of various sorts, especially composites and legumes, are very prominent; and the less palatable of these develop strongly after overgrazing. Besides the dominance of vast areas by grama grasses, the condition that most characterizes the true grassland is the occurrence of *Nolina, Dasylirion,* and *Yucca,* especially at lower elevations. These genera and *Microrhamnus ericoides* A. Gray and

Opuntia imbricata persist to higher elevations than any of the other desert-grassland transition species.

The transitional area is probably the least constant in the entire region, not only because of extensive interfingering with desert below and grassland above but also because the varied foothill region affords habitats not found in either desert or grassland and harbors plants equally unique. Guayule is such a plant. Of 7 sites where guayule was studied in detail, no 2 were quite alike in soil, topography, or associated plants. They all agreed in having abundant calcium and in exhibiting signs of shallow water penetration. No species except guayule and mariola occurred in all 7 habitats. Of 12 characteristic associated species, 6 belong principally to the desert vegetation and 6 to the transition or to the grassland. One species or another of *Bouteloua* characterized every stand of guayule ever seen in trans-Pecos Texas, although heavy grazing in some localities had restricted the grasses to relic occurrence in protected spots.

COMPETITION

Cannon (*4, p. 66*) concluded that in extreme desert situations there exists no competition between perennial plants, but only a struggle on the part of each individual to survive in the rigorous habitat. In less extreme deserts he believed there is root competition. In the American desert regions there are all gradations of competition and in the more extremely rigorous areas no competition at all. It is precisely upon this lack of competition that the failure of plant succession in extreme desert hinges. As pointed out by Muller (*12*), in truly desert situations plant succession is not operative and all manner of disturbance fails to initiate the phenomenon. Thus, in the true desert well below the transitional zone occupied by guayule, no competition between plants exists; along the upper limits of the desert, in the transitional zone, and in the grassland above, competition becomes progressively more severe.

Competition, when it exists in desert regions, is seasonal. Plants that remain dormant a large proportion of the year are not affected by competition during their periods of dormancy. In the native guayule habitats, furthermore, there is little competition for space and none for light, air, or similar factors. Competition takes the form of a race to absorb the limited moisture supply during the short period when it is available.

Some of the species most commonly associated with guayule are named as follows approximately in the order of decreasing competitive importance: *Bouteloua breviseta* Vasey, *B. gracilis, Agave lecheguilla, Aristida purpurea* Nutt., *Parthenium incanum, Coldenia canescens* DC., *C. greggii* A. Gray, *Opuntia* spp., *Jatropha dioica, Microrhamnus ericoides,* and *Leucophyllum minus* A. Gray. The three grasses are elements of grassland communities. *Leucophyllum* is a more or less obligate species of the transition, and the remainder are either ubiquitous or outposts of the desert vegetation. Also present are *Larrea, Acacia constricta* Benth., *Mortonia scabrella* A. Gray, *Fouquieria splendens,* and *Koeberlinia spinosa* Zucc., but these cannot be listed as important competitors of guayule. Their deep or sparse root habits make them completely innocuous to the shallow-rooted guayule, and very close proximity to these species produces no appreciable inhibition of guayule. With the exception of *Agave lecheguilla,* the desert species exert no great influence on guayule growth. In fact, desert populations offer slight competition to the species, and it is only the inherent rigor of the habitat that prevents the occupation of desert sites by guayule.

The competitive action to which guayule is vulnerable is depletion of moisture from the soil volume occupied by its roots. Evidence indicates that guayule requires a considerable soil-moisture content for active growth. During its growing season, the semidesert hills are briefly moist and cool and the habitat resembles that of a truly mesophytic vegetation. Lacking severe competition, guayule becomes perceptibly active in about 2 weeks after rainfall and continues to grow for about a month. If another significant precipitation should prolong the moisture availability, growth continues. However, under very severe competition the moisture supply may last only half as long, and growth is correspondingly curtailed. As the soil moisture is depleted, guayule is among the first species to cease active growth. Some of the other shallow-rooted shrubs, such as *Coldenia greggii*, remain active longer, while the deep-rooted species such as *Acacia* are unaffected by depletion of soil moisture in the horizons occupied by guayule and *Coldenia* roots. The habitat requires of the plant the ability to persist through prolonged periods of desert conditions interspersed with shorter periods of mesic conditions. The shortness of the latter periods requires the plant to absorb moisture promptly and rapidly.

The strongest competitors of guayule are the grasses, for they permeate thoroughly the upper soil levels occupied by guayule roots and deplete the soil moisture much more rapidly than do the less fibrous-rooted shrubs. *Agave* shares with the grasses the fibrous root habit and is therefore almost as strong a competitor, as noted by Lloyd (*11, p. 37*). In figure 10 is illustrated the dense mass of fibrous roots subtending the rosettes of *Agave*, the widely spreading lateral roots, and a rhizome emerging to the right to form a new plant. *Yucca*, *Nolina*, and *Dasylirion* also are fibrous-rooted plants, but they occur only as scattered individuals and produce no mass effect, while both grasses and *Agave* grow in dense stands and thus amplify their desiccating action.

Clements, Weaver, and Hanson (*5, p. 326*) stated: "It is improbable that competition for room exists as such, energy and material being the actual factors in all the instances known." The nature of competition offered by *Agave lecheguilla* probably is an exception to this statement. True, the most severe competitive action of *Agave* consists in its removal of soil moisture by means of its dense fibrous root system. However, in spite of this form of competition, other species, including even guayule, can persist and grow in small spaces surrounded by solid masses of *Agave*. Within the solid masses, on the other hand, access to the soil surface is denied any invader by the sheer density of the fleshy rosettes of *Agave*. Similarly, *Dasylirion* effectively holds an area by the great density of its dead leaves. Although these leaves use no light themselves, they exclude all other plants not only by intercepting all the light but also by simply occupying all the space at the soil surface. In either case guayule and other species are effectively restrained from even reaching the soil surface thus held.

Weaver (*17*) pointed out that the concentration of feeder roots of grasses, particularly in the drier westerly grassland region, is in the upper few feet of soil. He remarked the importance of layering in the community structure, deep-rooted forbs absorbing from levels below those

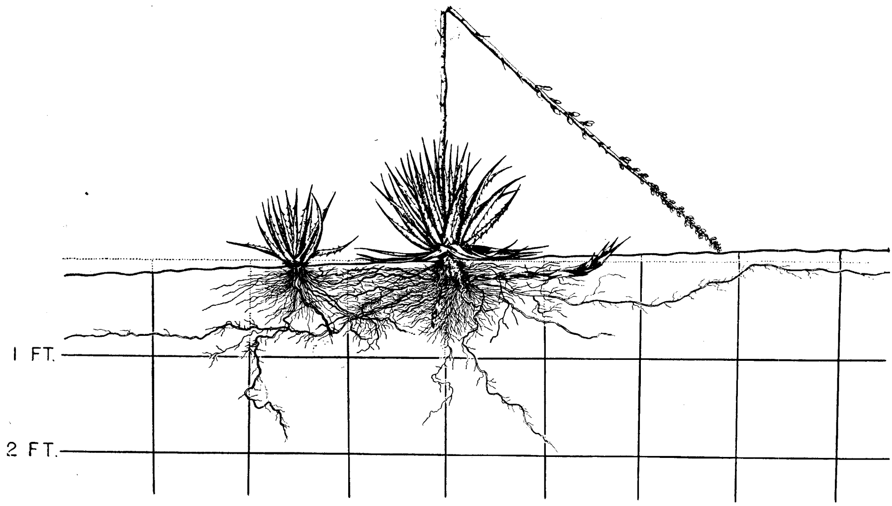

FIGURE 10.—*Agave lecheguilla* growing immediately to the right of the guayule plants shown in figure 11. This species is one of the most effective competitors of native guayule. Note the dense fibrous root system, the widely spreading principal roots, and the rhizomatous habit of vegetative reproduction.

occupied by dense grass roots. He further stated (*p. 147*) that "no 'hardpan' was encountered where mechanical resistance was so great that roots could not penetrate." Guayule is a species with an obligate shallow root habit in its native habitat. The shallow percolation of water and the inability of the plant to penetrate the characteristic hardpan of the area studied confine the roots to the upper levels where they are thrown into direct competition with grass and *Agave* roots. The species does not share with the deep-rooted shrubs the ability to push through resistant soil layers and thus outdistance the competing grass roots.

The effect of competition on guayule varies with its intensity and with the identity of the competing species. In figure 11 are illustrated two guayule shrubs about 20 years old growing in the 02 Ranch locality. Note that their encroachment upon each other is limited and that there is a tendency for each to spread in the opposite direction from the other. The plant on the left was subjected to light competition from *Bouteloua breviseta, Dalea frutescens* A. Gray, and *Lycium berlandieri* Dunal growing about 3 feet to the left. The plant on the right, on the other hand, was closely crowded (within 1 foot) on the right by a rosette of *Agave* and a large clump of *Bouteloua*. Competition by these resulted in poor root development and the reduced growth of the shrub. The root development should be compared with that of a plant that had become well established before competition developed severely and that at the time of excavation was subjected to only moderate competition by scattered *Agave* (fig. 1).

A growth-ring analysis of the two guayule plants in figure 11 revealed the basis of the difference in diameters of their stems. The diameter of the xylem of the plant on the left was 22.5 mm.; that of the one on the right, 17.25 mm. Polished cross sections of stems viewed under a dis-

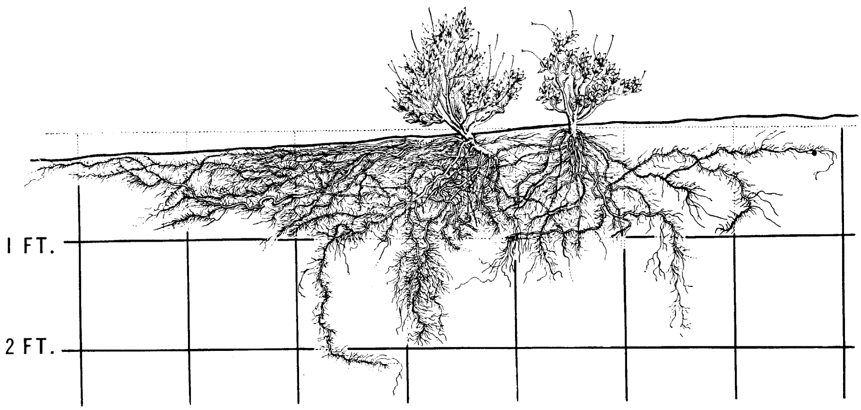

FIGURE 11.—Native 20-year-old plants of guayule in Ector stony loam in Brewster County, Tex. The larger plant developed without serious competition, but the stunted one was crowded (within 1 foot) on the right by *Agave lecheguilla* and *Bouteloua breviseta.*

secting microscope readily revealed the identities of annual and secondary rings. Relatively accurate counts set the age of these plants at about 20 years. Correlation of recognizable rings in these two stems was easy. In the comparison it was noted (1) that there were no cases of absence of an annual ring, (2) that secondary rings (representing resumptions of growth resulting from effective rains) were common in both, and (3) that in the stunted plant these secondary rings were sometimes unrecognizable. In a series of 12 identifiable annual rings the larger plant exhibited 15 such secondary rings, while in the corresponding 12 annual rings of the stunted plant only 7 secondary rings appeared. Competition, therefore, had made ineffectual some of the less heavy rainfalls.

Under very severe competition even some of the annual rings may be missing. A series of 26 plants growing under very heavy competition in the 02 Ranch locality was compared with 30 plants growing under little or no competition in the same area. Ring analyses of these plants showed ready correlation of principal rings within each group, but correlation between groups was difficult. In spite of the very stunted appearance of the competing plants, their stem diameters per number of rings of all classes visible (growth increments) were not significantly different from those of the noncompeting plants. Competition apparently had eliminated not only most of the secondary growth periods but had even made ineffectual some of the less pronounced annual rainy seasons, thus raising the average size of the visible growth rings. Ring analysis, therefore, is relatively unreliable for the determination of the age of guayule grown under severe competition unless correlation with a neighboring plant free of competition is possible.

The growth of guayule may be considered directly comparable with the length of time that favorable temperatures coincide with an adequate supply of moisture. During such periods the plant functions as a mesophyte. When moisture is depleted, it reacts by cessation of growth, loss of leaves, and tolerance of drought by elimination of almost all water-requiring activities. During that period it functions as a true xerophyte.

This dual ability represents no essential change in the nature of the plant but rather an expression of a wide range of tolerance. In its native habitat guayule is required to be a xerophyte more than three-fourths of every year. Heavy competition may further reduce its period of growth by more rapid depletion of moisture.

In deep soils certain species of the guayule region reach adequate moisture over a longer period than do the shallow-rooted species. *Prosopis velutina*, *Bernardia obovata* Johnst., *Viguiera stenoloba* Blake, *Dalea frutescens*, *Acacia constricta*, *Ephedra aspera* Engelm., and *Mimosa biuncifera* Benth. all showed growth activities in the spring of the year, even though the surface 4 feet of soil was powder-dry as a result of failure of spring rains and the shallow-rooted species remained dormant. Even intermingled with dormant guayule such species exhibited this evidence of a deep-rooted habit. It may be concluded from this that they possess a greater vigor of growth whereby they are capable of penetrating the very hard subsoil to reach the reservoir of moisture beneath.

Deep soils with only moderate runoff are particularly favorable for the deep-rooted species, and these grow in unusually dense stands on such sites, frequently associated with a sod of grasses. That guayule too can thrive under these physical conditions is clear from its response to cultivation and from the luxuriance of the occasional waif that invades the thickets of deep-rooted shrubs and finds some niche not too subject to competition. However, by their very density the other species so occupy the soil that guayule can accomplish ecesis only rarely. The adjacent rocky slopes are much less favorable for the deep-rooted shrubs and offer guayule a multitude of niches free of severe competition.

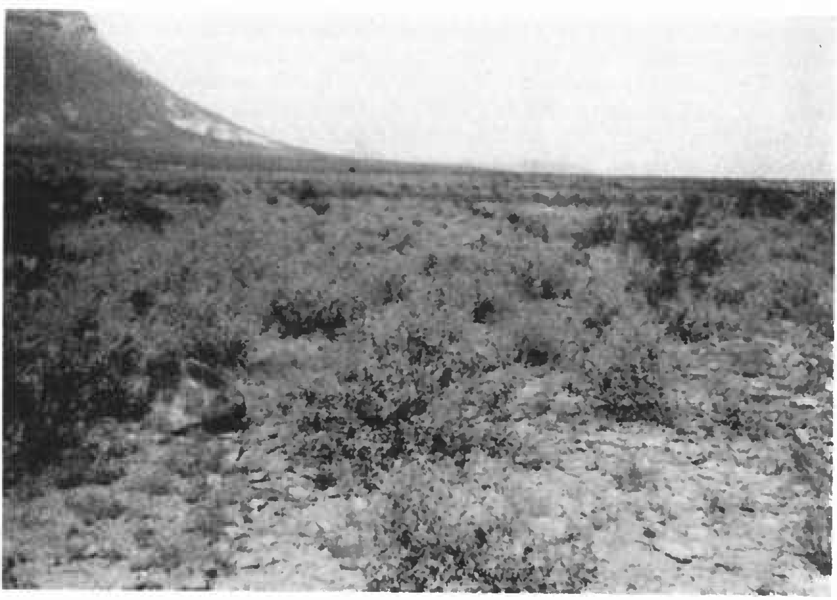

FIGURE 12.—A society of mariola in an area dominated by guayule. The two species alternate in dominance or intermingle without apparent cause or perceptible site differences.

In summary, it may be said that the lower regional altitudinal limit of guayule is set not by competition but by the severity of the desert climate. Its upper limit is fixed by competition with highly developed grassland communities. Its local distribution between these limits is determined in part by the presence of suitable sites on the rocky slopes where competition is limited.

Local distribution, however, seems to relate to no perceptible cause. Apparently homogeneous areas bear patches of guayule alternating with those of mariola or other species. In figure 12 is shown a stand of mariola growing immediately adjacent to a patch of guayule (fig. 13). There was no perceptible difference in slope or soil surface to account for the alternation. Since the root habits of guayule and mariola are similar, soil differences could scarcely be responsible. It might be hypothecated that the ecesis of one or the other species was favored by some now unrecognizable factor of the habitat or accident of dispersal and that the advantage of prior occupation has enabled each to resist invasion by the other.

DISTURBANCE

Two major kinds of disturbance have affected guayule adversely in trans-Pecos Texas. They are exploitation by man for rubber and browsing by animals. In the more favorable sites controlled exploitation need not be detrimental to native stands. If the harvest is kept within the limits of reestablishment and growth increment, no harm to the stand results. When the efficiency of reestablishment is impaired by drought, competition, or browsing, the percentage of the stand eligible for harvest may be very low indeed.

FIGURE 13.—Native guayule and associated species heavily grazed by cattle on Bandera Mesa, Presidio County, Tex.

If exploitation is restricted to the harvesting of mature plants and of these only where reproduction is obviously good, the stand will eventually recover sufficiently to permit a second harvest. For instance, certain areas in trans-Pecos Texas yielded a good harvest in 1943 and 1944 in spite of having been exploited in 1925. However, vast areas from which shrub was harvested during 1925 bore little or no guayule at the later date.

A site 6 miles west of Dryden, Terrell County, had a good stand of mature plants. This site was more than usually subject to protracted periods of drought, and guayule persisted there as a relic of a more favorable period. It was not reproducing itself at all, and harvesting of the mature shrub would have resulted in extermination of the stand.

The effect of severe browsing can be seen by comparing two localities on the mesa slopes near Balmorhea and Fort Stockton. Both were exploited in 1925, and both exhibited fair stands as late as 1942. The Balmorhea site is the same on which root studies were made. It yielded a good harvest in 1944, and, because reproduction was excellent, the stand was not impaired. Browsing here was restricted to the limited nibbling of cattle, and, although the range was overgrazed, the resulting harm to guayule was negligible. The second site is at the east end of Sevenmile Mesa, east of Fort Stockton. This area was heavily overbrowsed by goats. In 1942 a fairly dense stand of badly eaten guayule was still in evidence. Flowering was rarely permitted by the browsing animals, and seedlings younger than 6 or 7 years could not be found. In 1944 a careful search revealed two living plants in the entire locality.

Browsing by goats and sheep is much worse than that by cattle. Only during seasons of great stress will cattle bother guayule even moderately. Deer and jack rabbits are very similar to cattle in their effect on guayule.

FIGURE 14.—Undisturbed native guayule adjacent to that shown in figure 13. Note the luxuriance of guayule foliage and grasses.

Protection from cattle results in much more luxuriant growth, but reproduction is excellent with or without protection. In figure 13 is shown a heavily grazed site on Bandera Mesa, Presidio County. Note the very sparse grass and the relatively small shrubs of guayule. Figure 14 is a view of ungrazed land immediately adjacent. Note the luxuriance of both grass and guayule. Reproduction by seedlings was equally excellent on both sides of the intervening fence. Browsing by cattle carries no threat of extermination, but it effectively reduces the rate of growth.

ECOLOGY OF CULTIVATED GUAYULE

Although cultivation represents a high degree of specialization of habitat for guayule, it constitutes most of the interest in the species. The ecological aspects of cultivation, especially as related to root behavior, therefore occupied the greater part of this study.

Root Habit of Cultivated Guayule

In an effort to establish a "normal" of sorts as a basis for comparison, a generalization typical of a large number of well-developed, mature root systems grown under favorable conditions is described. Variations from this are correlated with habitat factors as they appear in the study. Admittedly there is no normal or typical root system. No two individuals are quite alike, and each is normal for its own growth conditions. However, a large number of plants were encountered that fell into a single general type of root system, and any great deviation from this type invariably seemed correlated with some unusual and frequently detrimental condition of habitat.

A great variety of soils, including the vast majority of the tilled ones of the southwestern United States, show the general characteristics of considerable depth, fair drainage, good aeration, penetrability, favorable fertility, and moderate water-holding capacity. In such soils the root development of guayule follows a fairly well-defined pattern that may be called normal. At any rate this pattern is common, characteristic of successful growth, and desirable in guayule culture. Not only soils but also water supply and competition serve to determine root habit. Assuming adequate water and uniform spacing, the normal type develops in a favorable soil. Examples of well-developed, mature root systems in various kinds of soil are illustrated in figures 15, 16, and 17.

Maturity is here defined rather arbitrarily as the stage of development and expression of gross morphology reached by a 2-year-old [3] cultivated plant, or one that has passed through two growing seasons. This would correspond in approximate size and stability of form to a native plant about 20 years old. A normal 2-year-old cultivated plant frequently has reached a root depth of at least 15 feet, and the other features of its root physiognomy are equally well advanced. No great changes in form can be expected to result from further time for growth, at least none comparable with those of the first and second years.

In mature guayule dominance has been lost by the taproot, and a large number of principal roots have developed. These branch repeatedly but

[3] Age of seedling plants was computed from the date of seeding, since presprouted seeds were used and emergence was immediate. Age of transplants was computed from the date of transplanting regardless of age of stock used; growth after transplanting rather promptly erased differences between the extremes of size and age classes of acceptable stock transplanted.

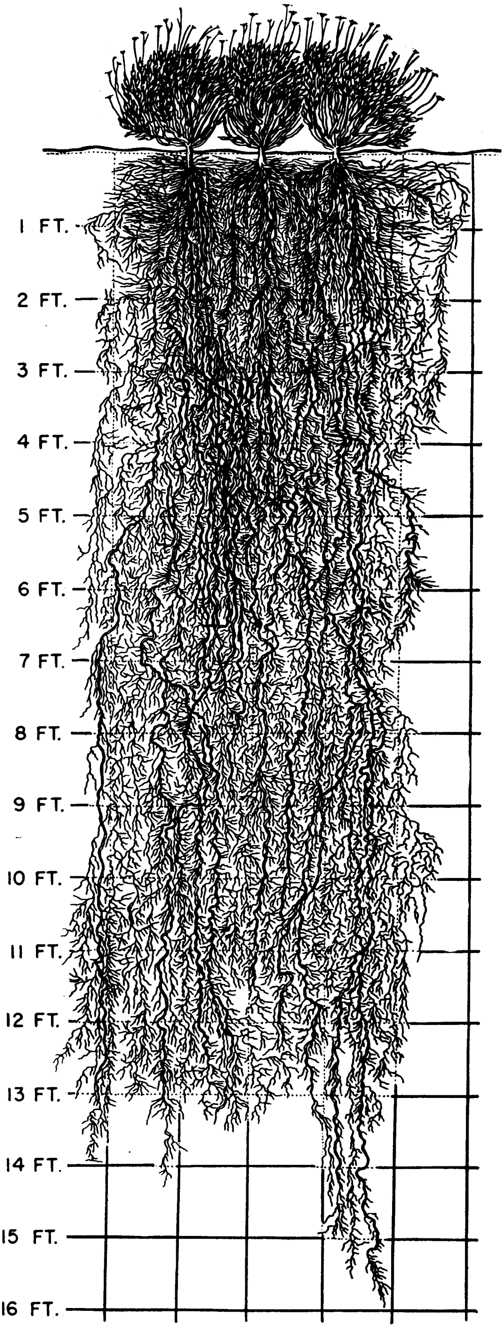

FIGURE 15.—Two-year-old guayule transplants spaced at 12 inches within the row and grown under irrigation in Anthony loam near Litchfield Park, Ariz.

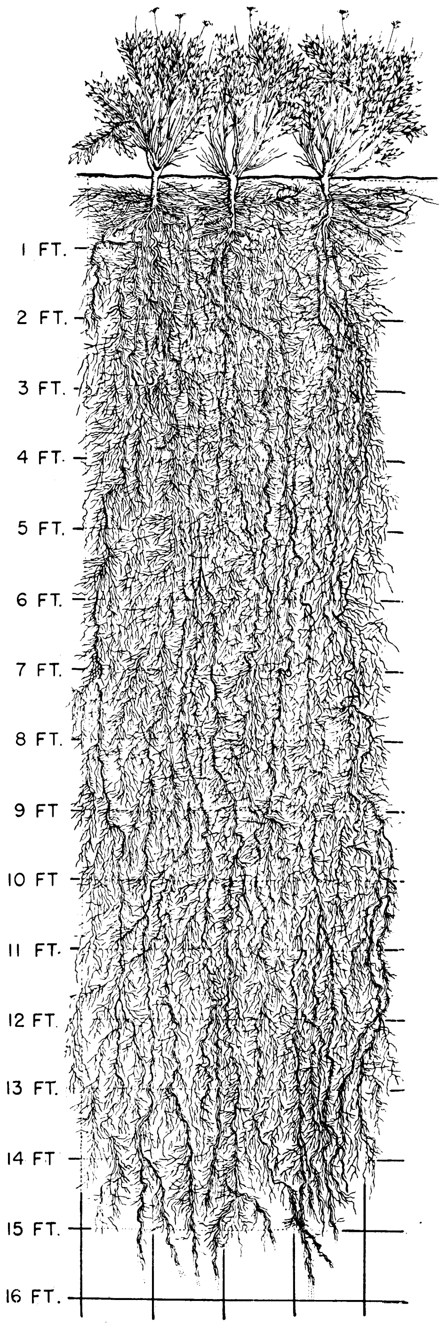

FIGURE 16.—Two-year-old guayule transplants spaced at 12 inches within the row and grown without irrigation in Lewisville silty clay at San Antonio, Tex.

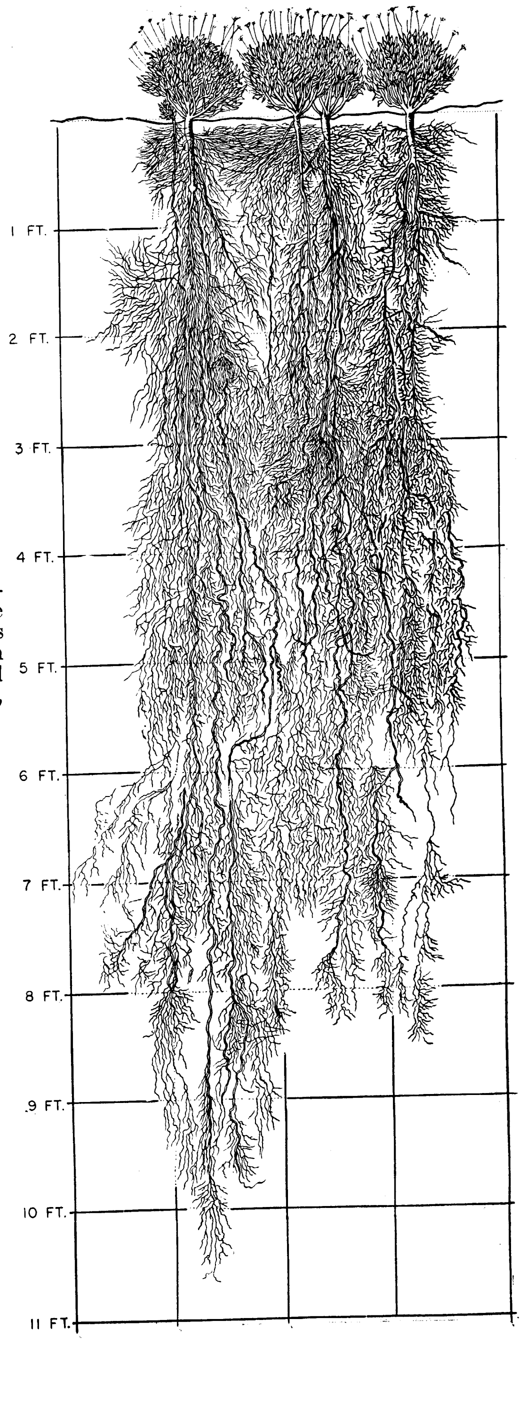

FIGURE 17.—Seventeen-month-old direct-seeded guayule spaced at about 10 inches within the row and grown under irrigation in Greenfield loam in the Salinas Valley, Calif.

maintain their identities as they progress downward. The prominence of laterals depends upon the available soil space; two adjacent even-aged plants divide the intervening space about equally. There is very little extensive overlapping of laterals, although intermingling of peripheral roots may be rather complete. This failure to overlap results in a rather strict habit, as though the entire system had been molded into an attenuate vertical cylinder. In undisturbed seeded plantings the mature root system exhibits a slightly stronger primary root, but at depths of 2 to 4 feet this is indistinguishable from the several principal secondary roots. Contrast figure 17, which shows a direct-seeded planting 17 months old (including two growing seasons), with figure 71 (p. 81), which shows 2-year-old transplants from a nearby plot.

The principal roots, or secondaries, give rise to a dense growth of tertiaries, quaternaries, and so forth, some of which may assume the roles of principal roots and persist through a long downward growth. A dense production of absorbing branches throughout the root system results in relatively complete occupation of the soil volume.

The depth of root growth is so completely dependent upon the depth of favorable soil that no normal depth may be named. All of the well-developed, fairly mature root systems observed shared the character of very deep penetration, ranging from 15 to 20 feet. All of these, furthermore, passed through soil layers of considerable resistance. Some were observed to terminate in such layers, and it is merely a matter of conjecture whether they might not have reached much greater depths had resistant soil layers been absent. In the Salinas Valley, Calif., several excavations of 2-year-old plants revealed relatively shallow root systems correlated with a subsoil of coarse sand. Figures 17 and 71 (p. 81) represent plants from such situations that reached maximum depths of approximately 11 and 8 feet, respectively.

Chronology of Seedling Development

Because growth rate is so dependent upon the season of the year and the factors that vary with weather, the development observed during one season would not be exactly indicative of that to be expected during another. Further, the behavior of seedlings in one climate would not parallel exactly that in another. Under cultivation and irrigation, however, growth conditions during the most favorable season of the year would be rather similar in the various regions adapted to the growth of guayule. A series of observations made in the Salinas Valley during July, August, and September, 1944, constitute an accurate characterization of the rate and nature of root development during the favorable season of the year in that district. In warmer and drier climates greater rapidity of development under irrigation is to be expected.

For the purpose of studying seedling development, a planting was made in Greenfield fine gravelly loam in the Salinas Valley on July 5, 1944. The seedbed had been carefully prepared and preirrigated. Standard-treated seed was drilled in by standard methods, and the soil was kept moist by furrow irrigation as required. The plot was kept completely free of weeds by hand weeding. Beginning 5 days after seeding, excavations were made at semiweekly intervals until the twelfth day, then at weekly intervals until the plants were 40 days old, and finally at biweekly intervals until the sixty-eighth day after planting. When the plants were about 6 weeks old competition became severe, and the stand was thinned to single plants at 20-inch intervals within the row on August 23. This, too, corresponds to standard practice. Prior to the thinning, each excavation involved a sample of a single row 6 to 10 inches long. The seedlings were drawn in natural position. The samples, chosen with care to represent average conditions in the plot, included both well-advanced and somewhat retarded individuals and in no case consisted of either the smallest or the largest plants. After the thinning, each sample consisted of three adjacent plants within a single row; the same precautions were observed in choosing the plants.

In following the root development of seedlings through a period of 68 days, it was noted that in that time the roots had ramified through a considerable volume of soil to a maximum depth of nearly 3 feet. However, retarded individuals were not nearly so deep, and irregularity of growth and penetration characterizes all stages of early root development. In general, during the more favorable season 2 months of growth is ample for ecesis of the plants, and critical care in weeding and irrigating is thereafter of less extreme importance.

Since the seed treatment prior to planting involved soaking until about 5 percent of the seeds were beginning to germinate, germination in the field was very prompt. In figure 18 are illustrated the germinating seeds

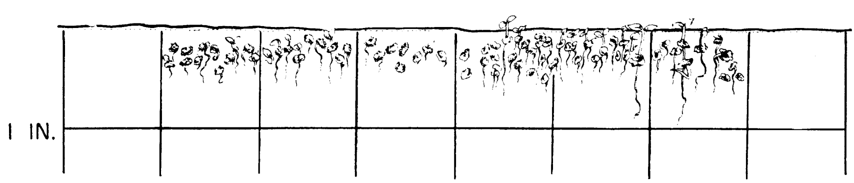

FIGURE 18.—Five-day-old seedlings of guayule growing in the Salinas Valley, Calif., July 10, 1944.

5 days after planting. Note that although some of the radicles were about three-fourths of an inch in length, no lateral branches had been produced. It is also noteworthy that the plants ranged from fully emerged individuals an inch in length to seeds with radicles just protruding.

A few seeds had just germinated on the eighth day after planting (fig. 19). Emergence from the soil was well advanced at this stage; the roots had grown as much as an inch in the intervening 3 days, but lateral branches were still lacking. On the twelfth day (fig. 20) the more ad-

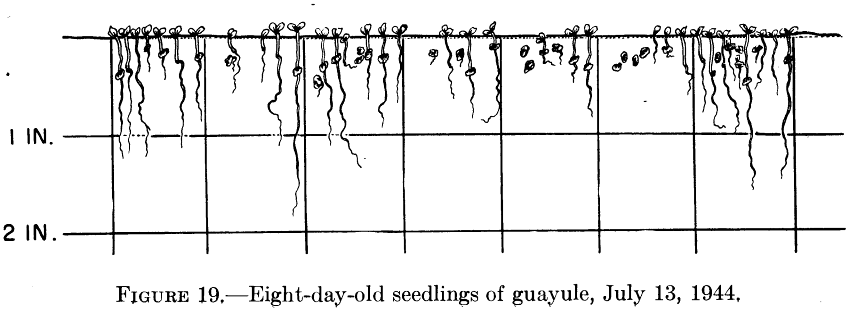

FIGURE 19.—Eight-day-old seedlings of guayule, July 13, 1944.

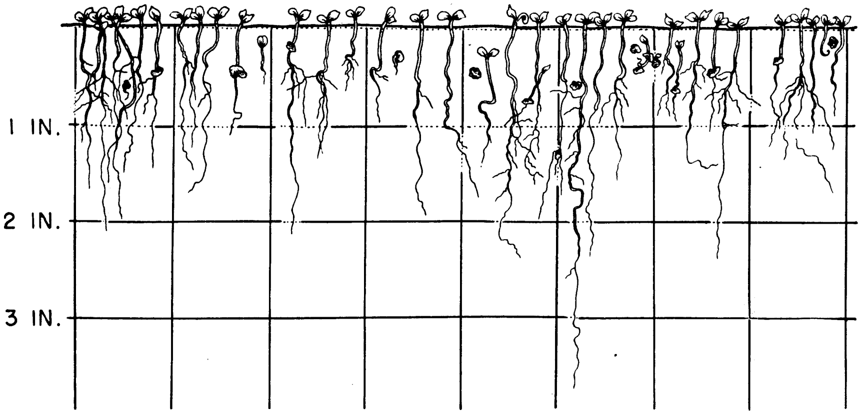

FIGURE 20.—Twelve-day-old seedlings of guayule, July 17, 1944.

vanced plants had produced a few true leaves, while some retarded seedlings were still emerging. The apparent anomaly of seedlings with expanded cotyledons below the soil level is explained by the presence of occasional fissures in the soil, which permit light to reach seedlings at those levels. The taproots of the more vigorous plants had reached depths of 2 to more than 3 inches. Lateral branches were very prominent at this stage, but they were very unevenly distributed. The long seedlings, with few short lateral roots and a clearly dominant taproot, were normal and healthy. The shorter ones, with the heavy development of laterals giving them the appearance of having a fibrous type of root system, had been diseased. Young seedlings in the Salinas Valley, if watered too copiously, are prone to develop seedling root rot, a disease that attacks the tip of the radicle (*3*). This results in the suppression of the taproot and the rapid growth of laterals, and in such plants the early taproot habit is quickly modified to a fibrous root habit. This response was also experimentally induced by cutting off the tips of healthy radicles and transplanting the seedlings in sand.

All the 19-day-old plants (fig. 21) had several true leaves and had shed their cotyledons. The irregularities in root penetration illustrated probably resulted mostly from the irregularity of germination, but genetic differences in rate of growth and the effects of seedling root rot might have been partially responsible. Whatever the cause, irregularity of penetration characterizes roots of guayule seedlings and no very definite rules may be laid down for determining their depth: this must be determined by investigation. Although the taproot habit was strong in some of the plants at 19 days, when some roots reached depths of 7 or 8 inches, many individuals with equal top development had root systems only about 2 inches deep. The latter are frequently characterized by a heavy development of lateral roots. This illustrates the fact that in young plants root normality cannot be deduced from top normality. In older plants, on the other hand, root abnormalities usually are clearly reflected in failure of top development.

The plants shown in figure 22 were 26 days old. Here, too, the irregularity of penetration was visible, about half of the seedlings having reached a depth of 8 inches and a few not more than 4 inches. Lateral

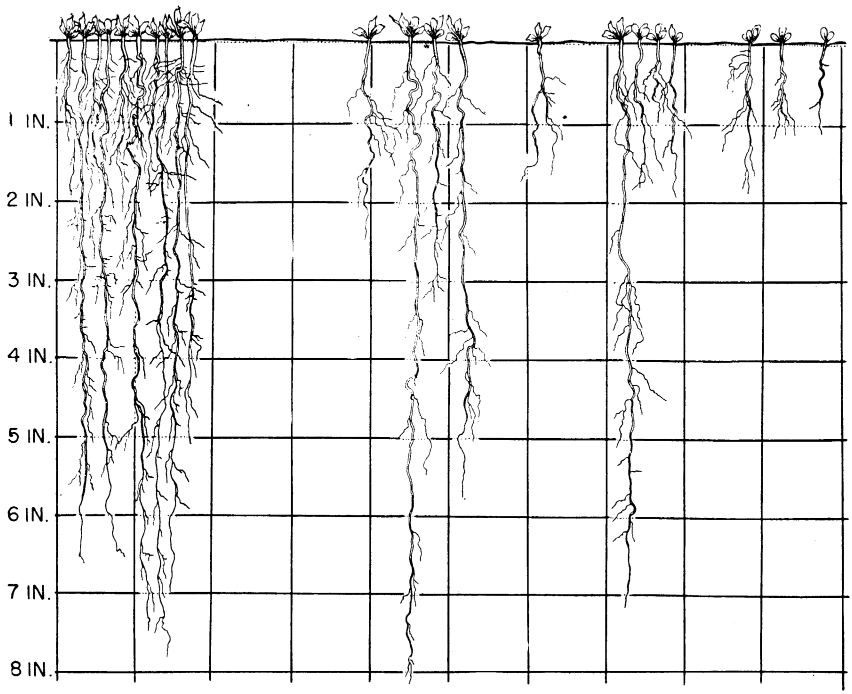

FIGURE 21.—Nineteen-day-old seedlings of guayule, July 24, 1944.

roots, except in the plants with inhibited taproots, were still very sparse and competition between adjacent seedlings was just beginning to appear.

The 33-day-old plants in figure 23 differed from the younger ones principally in the greater density of feeder roots, the secondaries produced at various levels by the primary root having branched copiously. This corresponded to a definite spurt of top growth observed.

The 40-day-old seedlings had developed markedly (fig. 24). The feeder roots were for the first time sufficiently dense to occupy the soil volume adequately, and top growth clearly reflected this degree of establishment. Competition, both above and below the soil level, had become rather acute, and the irregularity of growth seen at earlier stages had resulted in the complete dominance of retarded plants by the more advanced ones. Shortly after this sampling the stand was thinned to single plants at intervals of 20 inches in the rows, moderately well-developed plants being retained where there was a choice.

The 54-day-old plants illustrated in figure 25 had been relieved of competition for about a week at the time of sampling. Note the immediate response evidenced by the production of spreading laterals. In the 68-day-old plants shown in figure 26 the great density of feeders represents a consolidation of the advantage gained by removal of competition 3 weeks previously. These plants might have been regarded as well established. Their ecesis was sufficiently complete to insure their ability to withstand rigorous drought or such competition as heavy weed growth

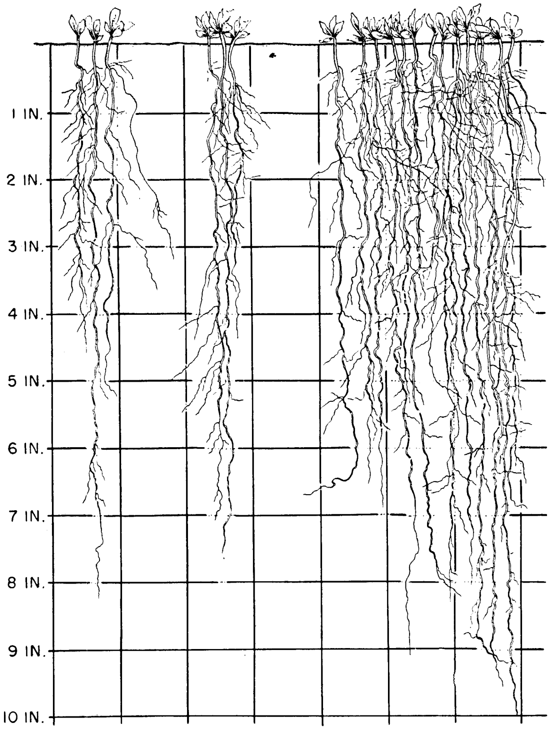

FIGURE 22.—Twenty-six-day-old seedlings of guayule, July 31, 1944.

without more serious consequence than the slowing or temporary stopping of their development.

The center plant in figure 26 may have been an individual retarded by seedling root rot, slow germination, or genetic slow growth. However, its roots had been trapped by hardening of the soil at about the 12-inch level. This hardening seems to require some time for completion; if the seedlings succeed in reaching a depth free of the hardening tendency (usually about 12 inches), they then develop normally below that depth despite the subsequent hardening of the soil above that level. Then, any influence, such as unfavorable season and low temperature, that might retard root penetration overlong in a soil prone to such hardening will result in the trapping of the root system by hard soil.

A plot managed very similarly to the one just discussed was planted on Bryant[4] loam on September 19, 1943. Excavations were made at weekly intervals, and biweekly examples of these are illustrated. In figure 27 are shown 15-day-old seedlings illustrating both irregularity of germination and the effects of seedling root rot, but the root development was in general comparable with that of the 12-day-old seedlings of the series discussed previously.

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[4] The Bryant soils have only recently been recognized in the field. As yet they have not been officially correlated by the Division of Soil Survey, Bureau of Plant Industry, Soils, and Agricultural Engineering.

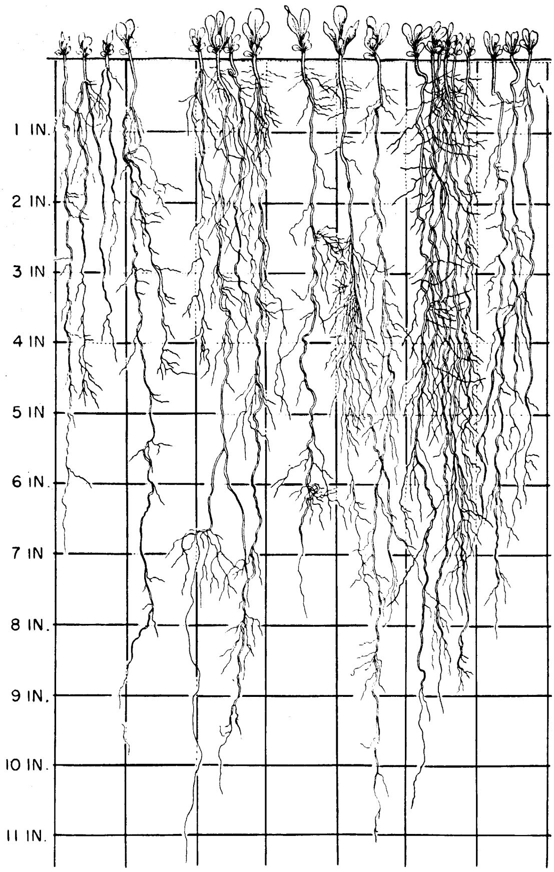

FIGURE 23.—Thirty-three-day-old seedlings of guayule, August 7, 1944.

The 29-day-old plants shown in figure 28 had a maximum root penetration of about 4 inches. This does not compare with the 8- and 10-inch penetrations of the 26-day-old plants shown in figure 22. Evidently the seasonal conditions in mid-October in the Salinas Valley had slowed the growth of these roots.

The roots of the 43-day-old plants shown in figure 29, although bearing fairly well developed laterals, had penetrated only 7 inches. The 40-day-old plants shown in figure 24, however, had reached 10- to 13-inch depths, had produced many more feeder roots, and had developed much more luxuriant top growth.

The 57-day-old plants illustrated in figure 30 showed extreme symptoms of having had their roots trapped by hardening of the soil. The numerous, short, crooked, thickened branches at the lower levels are characteristic of roots retarded by hard soil. The depth of these roots as compared with that of those in figure 29 reflects an error in choosing samples, but the shallowness of the root systems remains a significant

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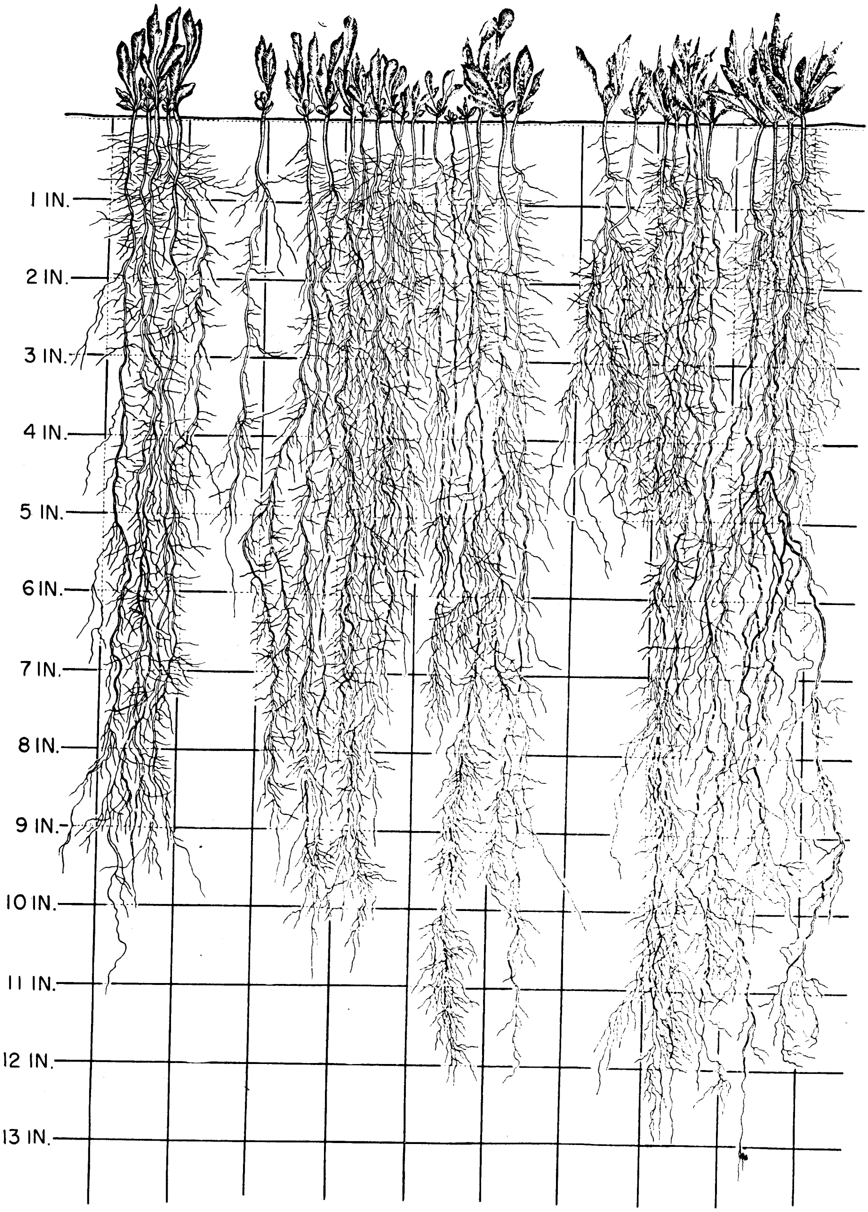

FIGURE 24.—Forty-day-old seedlings of guayule, August 14, 1944.

fact in both samples. With their small tops, 6-inch roots, and poor soil occupation, they are not comparable with the 54-day-old plants shown in figure 25, but from the standpoint of root penetration they correspond closely to the 19-day-old seedlings shown in figure 21.

In figure 31 the maximum root depths observed in the two series of

FIGURE 25.—Fifty-four-day-old seedlings of guayule, August 28, 1944.

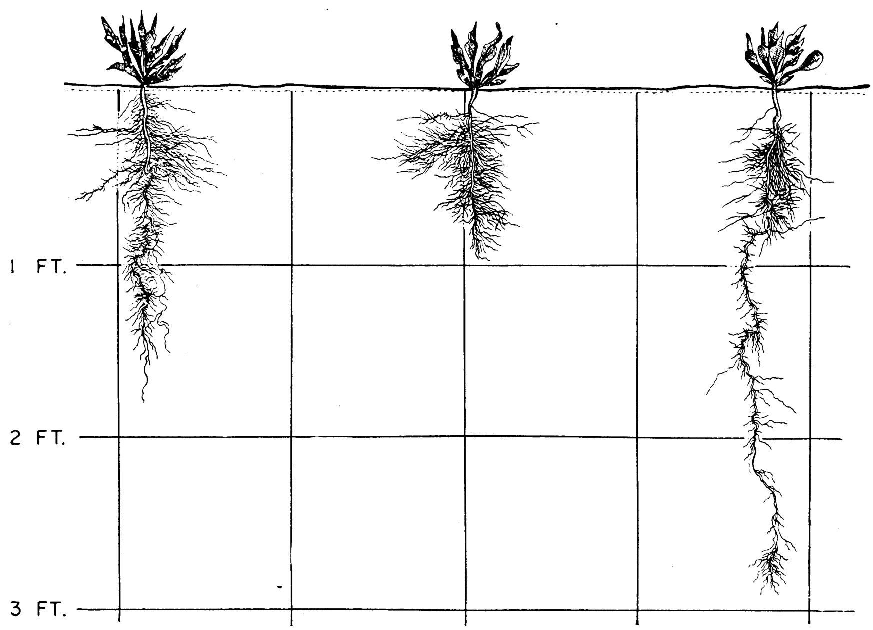

FIGURE 26.—Sixty-eight-day-old seedlings of guayule, September 11, 1944.

seedlings just described are plotted against the weekly average minimum temperatures recorded nearby. There is a strong correlation between the low average minima of the September-to-November season and the slow penetration of the 1943 seedling roots. On the other hand, the relatively steady higher temperatures of the July-to-September season of 1944 are reflected in the rapid penetration of seedling roots during that period.

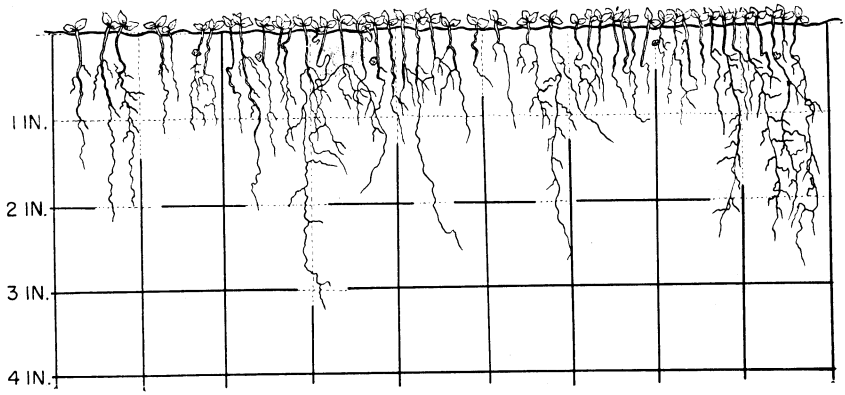

FIGURE 27.—Fifteen-day-old seedlings of guayule growing in the Salinas Valley, Calif., October 4, 1943.

As a result of having been planted so late in the season that only a few weeks of favorable growing weather remained, the plants of the 1943 series not only suffered a severe decrease in rate of growth but also were irreparably damaged by hardening of the soil. Observations during the summer of 1944 showed the remaining plants of this plot to be stunted in a manner characteristic of root binding. This phenomenon is more fully treated in the section on Effects of Soil Factors on Root Response.

COMPARATIVE GROWTH OF SEEDLINGS AND TRANSPLANTS

Simultaneously with the sowing of seed on July 5 for the study of root development, adjacent rows were planted to standard nursery stock spaced 20 inches apart in the rows. The stock was taken from 13-month-old nursery beds, had grown to good caliper (5/32 to 8/32

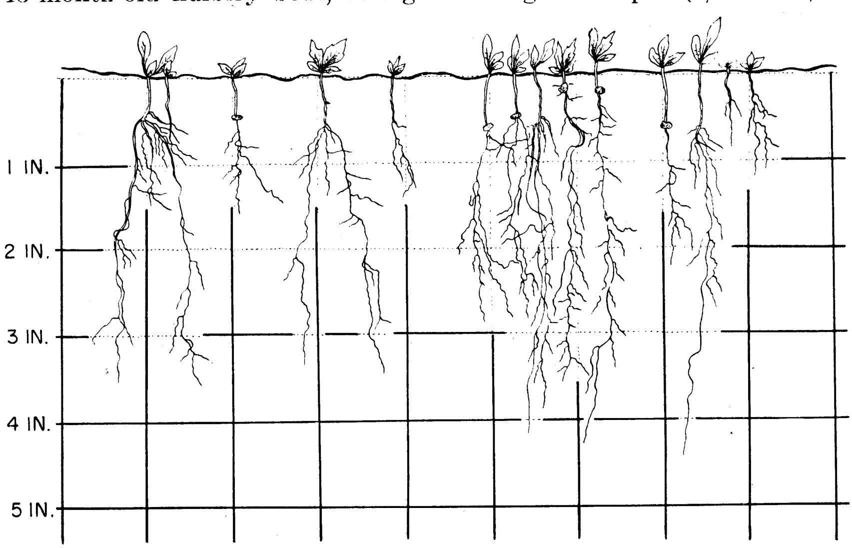

FIGURE 28.—Twenty-nine-day-old seedlings of guayule, October 18, 1943.

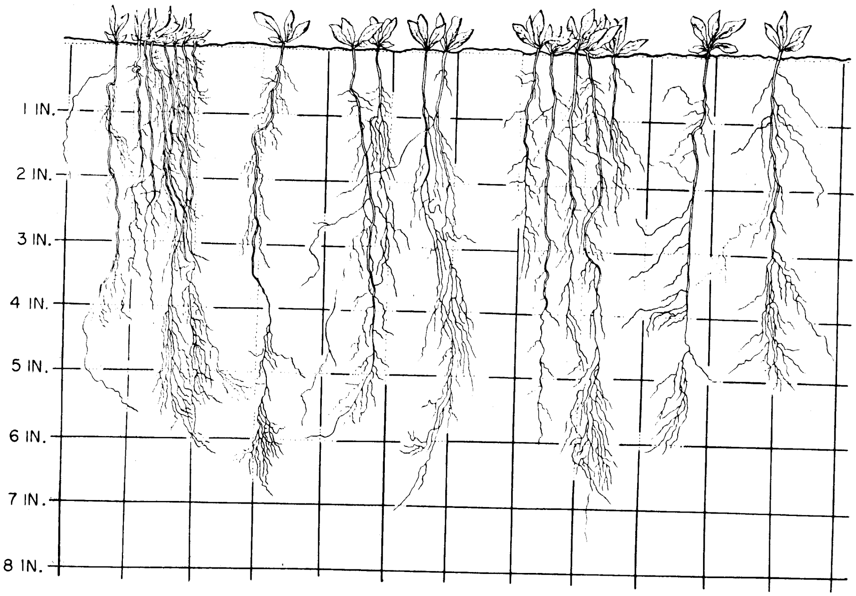

FIGURE 29.—Forty-three-day-old seedlings of guayule, November 1, 1943.

inch at the crown), and was well hardened off. It was in excellent condition, as evidenced by its prompt resumption of growth. The plot was

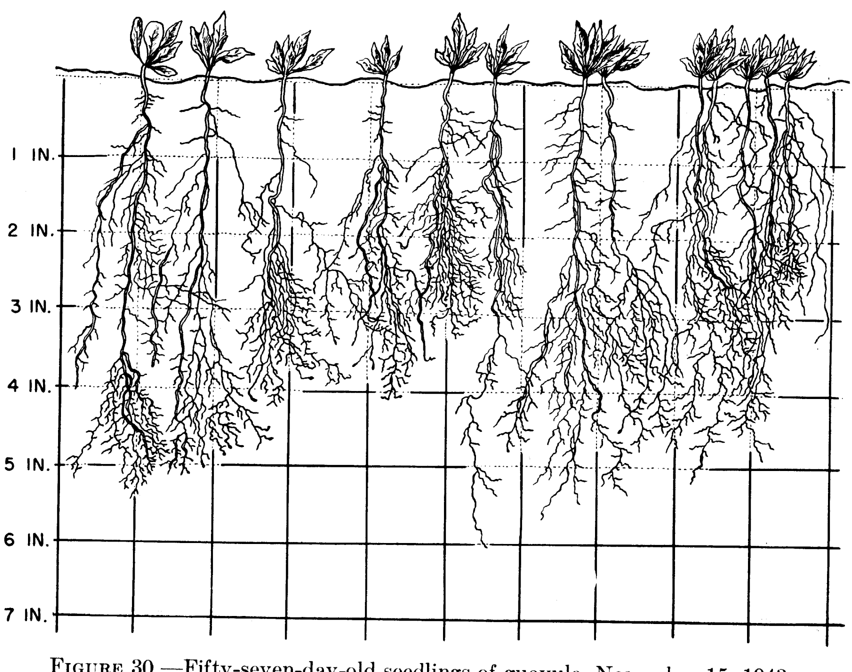

FIGURE 30.—Fifty-seven-day-old seedlings of guayule, November 15, 1943.

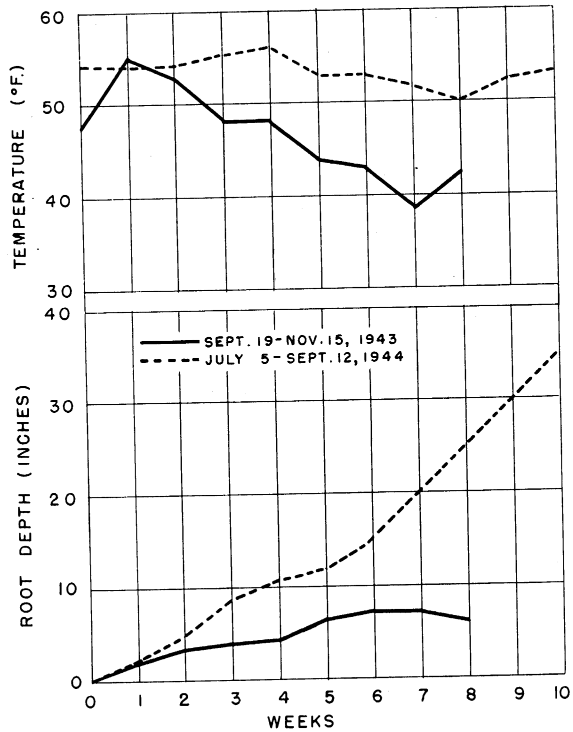

FIGURE 31.—Weekly average minimum temperatures and maximum root penetrations of guayule seedlings, 1943 and 1944.

kept free of weeds and adequately irrigated. Samples consisting of three representative plants were dug on the same days that the seedling plot was sampled. In all drawings of transplants prior to the fifty-fourth

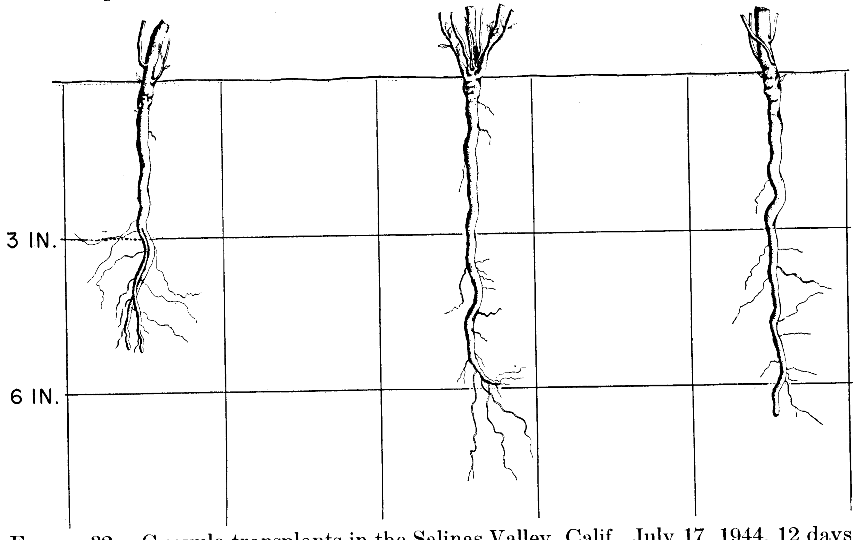

FIGURE 32.—Guayule transplants in the Salinas Valley, Calif., July 17, 1944, 12 days after transplanting.

day after planting, the plants were not drawn in actual relation to one another but were crowded together. Those of the fifty-fourth and sixty-eighth days were drawn in true position.

The rate of ecesis of transplants was somewhat greater than that of seedlings. Penetration in the two classes of plants remained nearly parallel, but the root systems of the transplants were characterized by greater spread and denser occupation of the soil. Ecesis was therefore considerably more complete in 2-month-old transplants than in seedlings of the same age. There is, however, a strong tendency for the two classes to equalize as they grow older, and in plants of several months' development the differences are scarcely discernible.

Inasmuch as the planting stock had roots about 6 inches long, no comparison of its root penetration with that of seedlings was possible until both kinds of plants were well advanced. For that reason the transplants excavated earliest are omitted from the discussion. In figure 32 are shown plants that had been in the ground 12 days. Each had produced several new roots, and the leaf buds were beginning to open. The transplants were partially leafed out 19 days after they were put in the ground (fig. 33), and the new roots were branching copiously; growth was beginning to increase the total depth.

Transplants were fully leafed out 26 days after they were set out and their roots had branched copiously enough to occupy the soil fairly well (fig. 34). Compared with 26-day-old seedlings (fig. 22), the transplants were quite advanced, as was to be expected, for their much greater bulk allowed a far greater supply of food materials to be used for root development. Since the plants were dug from the nursery after 13 months of growth, transplanting was for them merely a set-back in which they lost most of their tops and roots; they could recover from such injuries rather rapidly. In fact, it is surprising that transplants did not show a much

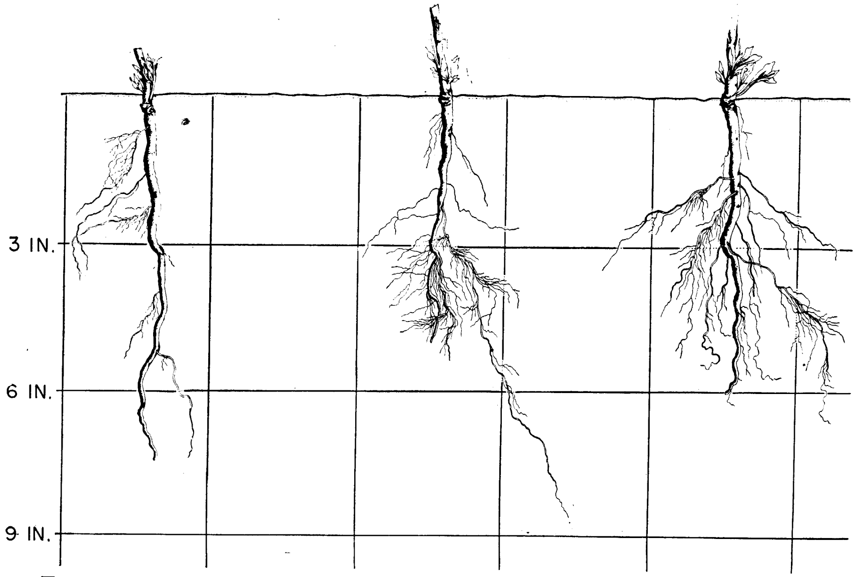

FIGURE 33.—Guayule transplants, July 24, 1944, 19 days after transplanting.

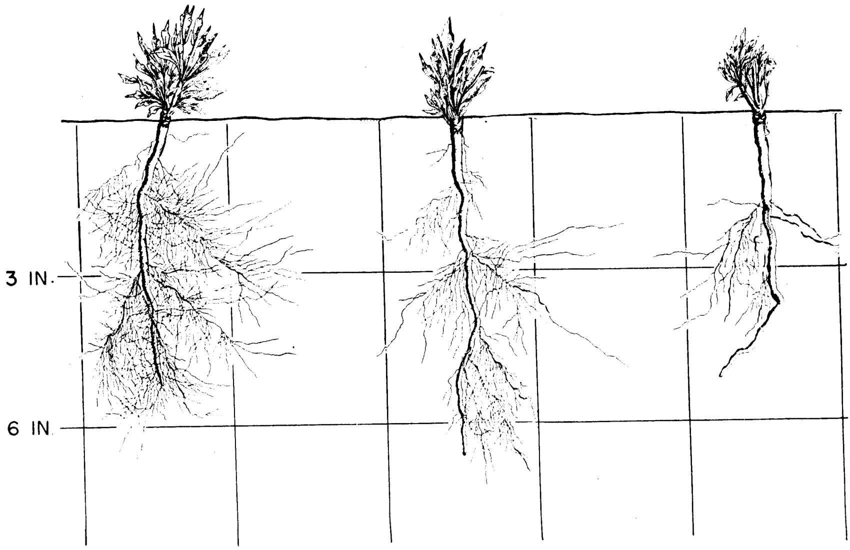

FIGURE 34.—Guayule transplants, July 31, 1944, 26 days after transplanting.

greater advantage over seedlings than they actually did.

In transplants that had been in the ground for 33 days, top growth had progressed considerably and root elongation and branching were well advanced (fig. 35). Similarly, the transplants that had been set out 40 days were establishing themselves apace (fig. 36). The most rapidly growing vertical roots had already obviously assumed the roles of principals and were producing lateral feeders prolifically.

In figure 37 are illustrated transplants 54 days after transplanting that had reached a stage of development which may be regarded as successful establishment. The early blooming of rapidly growing young plants is characteristic of the species. The densely branching root systems occupied the soil fully, as far as they reached. Compared with 54-day-old seedlings (fig. 25), the transplants were several times as large (in terms of leaf surface, wood, and breadth of root system). The depths of penetration, however, were very nearly the same.

In figure 38 are shown transplants that had been set out 68 days. The root systems had already assumed some of the characteristics of maturity, the several vertical principal roots forming a fibrous root habit very similar to the 2-year-old plants shown in figure 15. The advantage of the transplants over the seedlings was still very pronounced, but as the plants grow older the initial advantage of transplants over seedlings is progressively lessened by the great growth of both classes. However, judging by other excavations, it is not until the two classes of plants are over a year old that this advantage is fully obscured.

Comparative Growth of Transplants and Rooted Stem Cuttings

The root development of rooted stem cuttings was studied in comparison with standard transplanted nursery stock in a single excavation after the plants had had a full season's growth in the field. The early development of the cuttings was not observed. The cuttings had been rooted

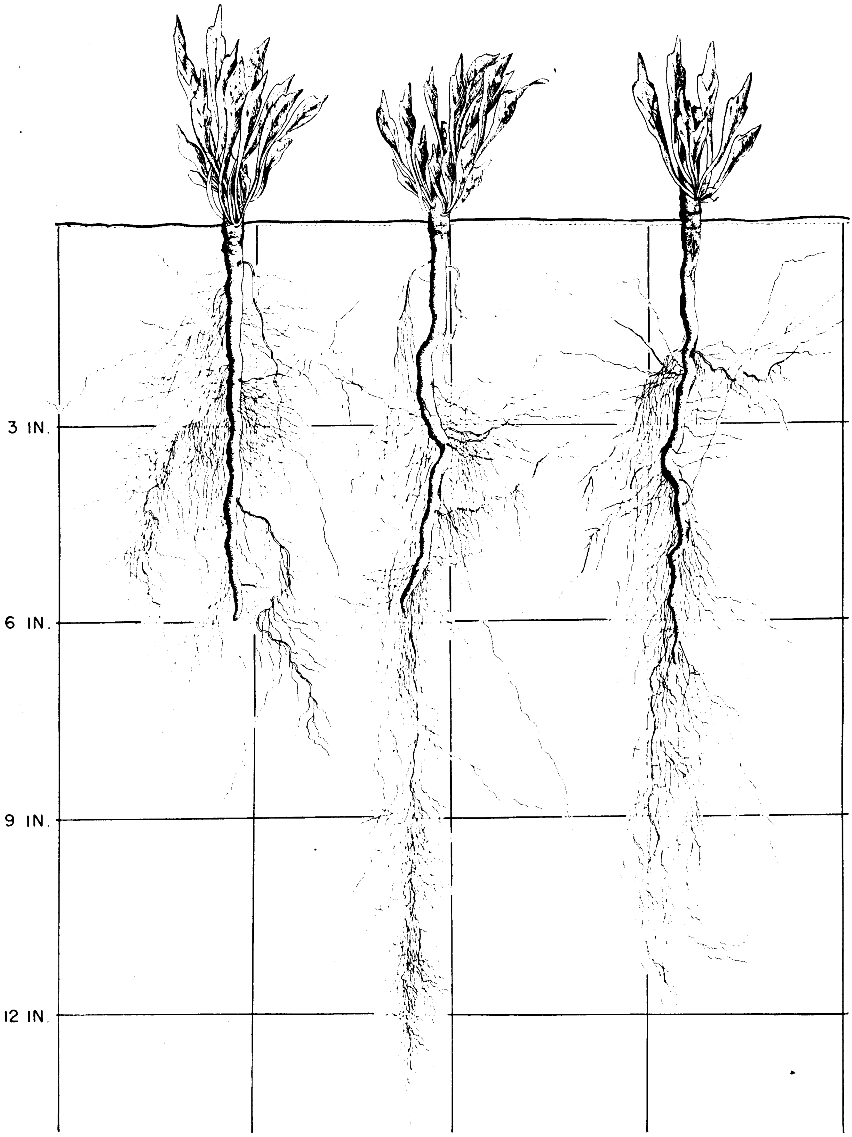

FIGURE 35.—Guayule transplants, August 7, 1944, 33 days after transplanting.

and grown in flats in the greenhouse for 5 weeks when, on June 5, 1943, they were transplanted to the field under irrigation. Simultaneously, adjacent rows were planted to standard nursery stock. The soil was a deep phase of Greenfield fine gravelly loam, a soil that is very favorable to root penetration. About December 20, 1943, after about 28 weeks of growth under irrigation, both plantings were sampled.

In figure 39 are illustrated the transplanted nursery plants. Their

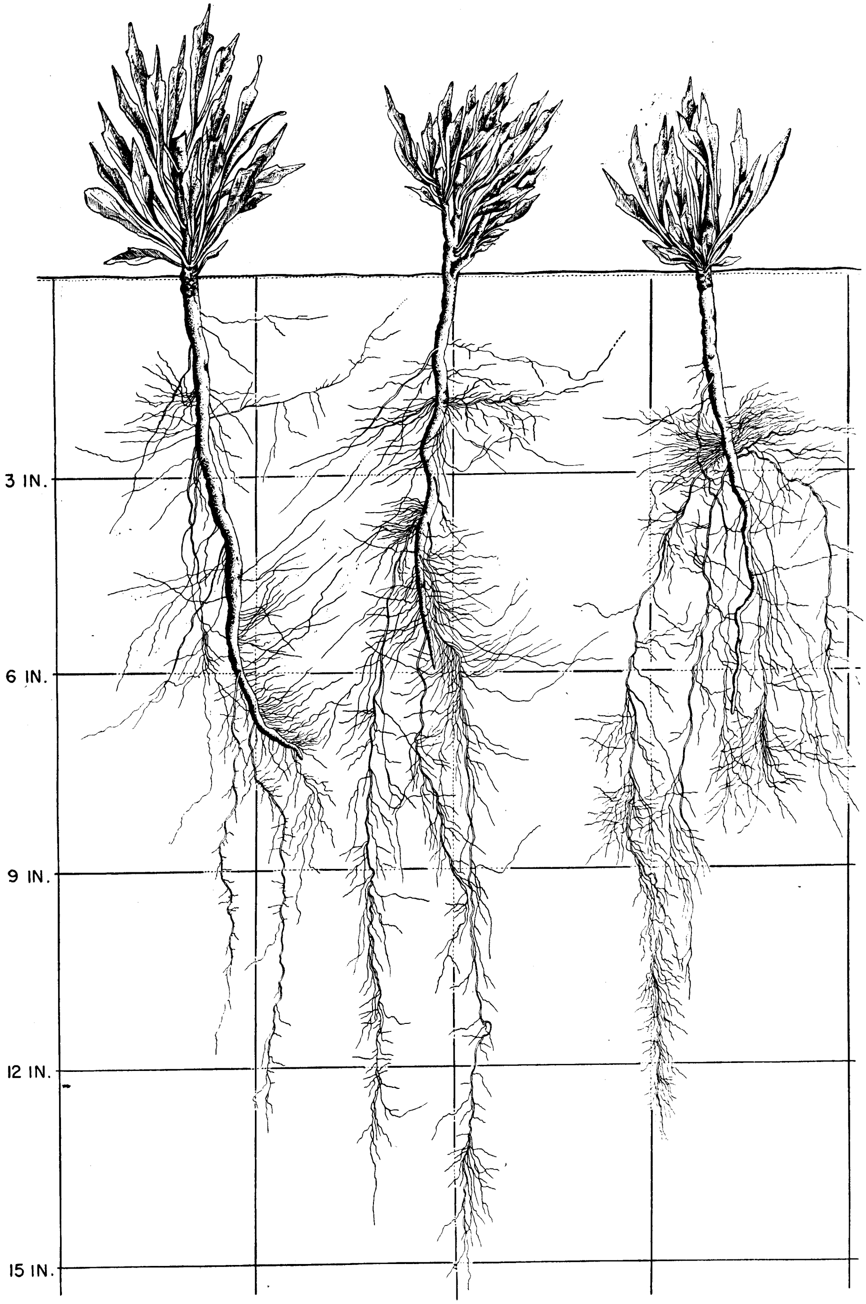

FIGURE 36.—Guayule transplants, August 14, 1944, 40 days after transplanting.

root systems were normal throughout, the depth of penetration, extension of laterals, and degree of occupation of the soil volume being good for this immature stage in their development. The transplanted stem cuttings are shown in figure 40. Their development was comparable in every way with that of the transplanted nursery stock, both top and root growth being about equal in the two classes. The initially greater size of the nursery stock had been rather completely obscured by one season's growth.

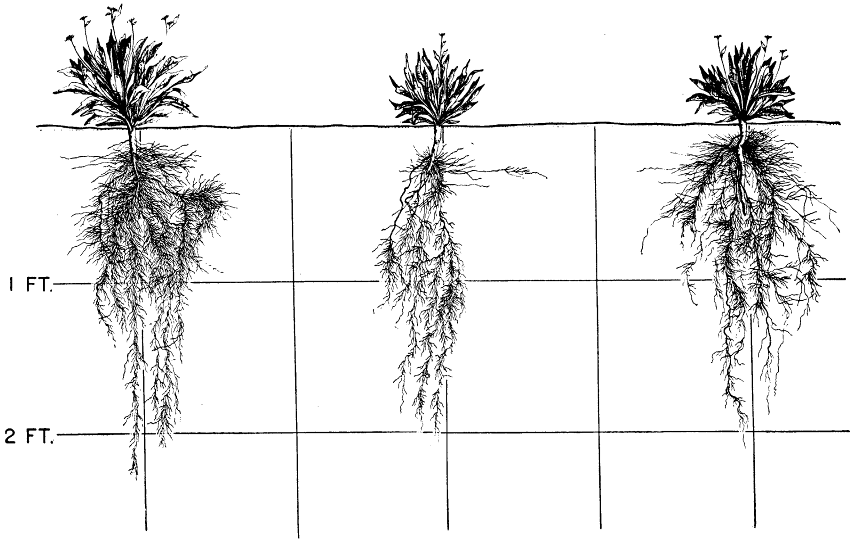

FIGURE 37.—Guayule transplants, August 28, 1944, 54 days after transplanting.

FIGURE 38.—Guayule transplants, September 11, 1944, 68 days after transplanting.

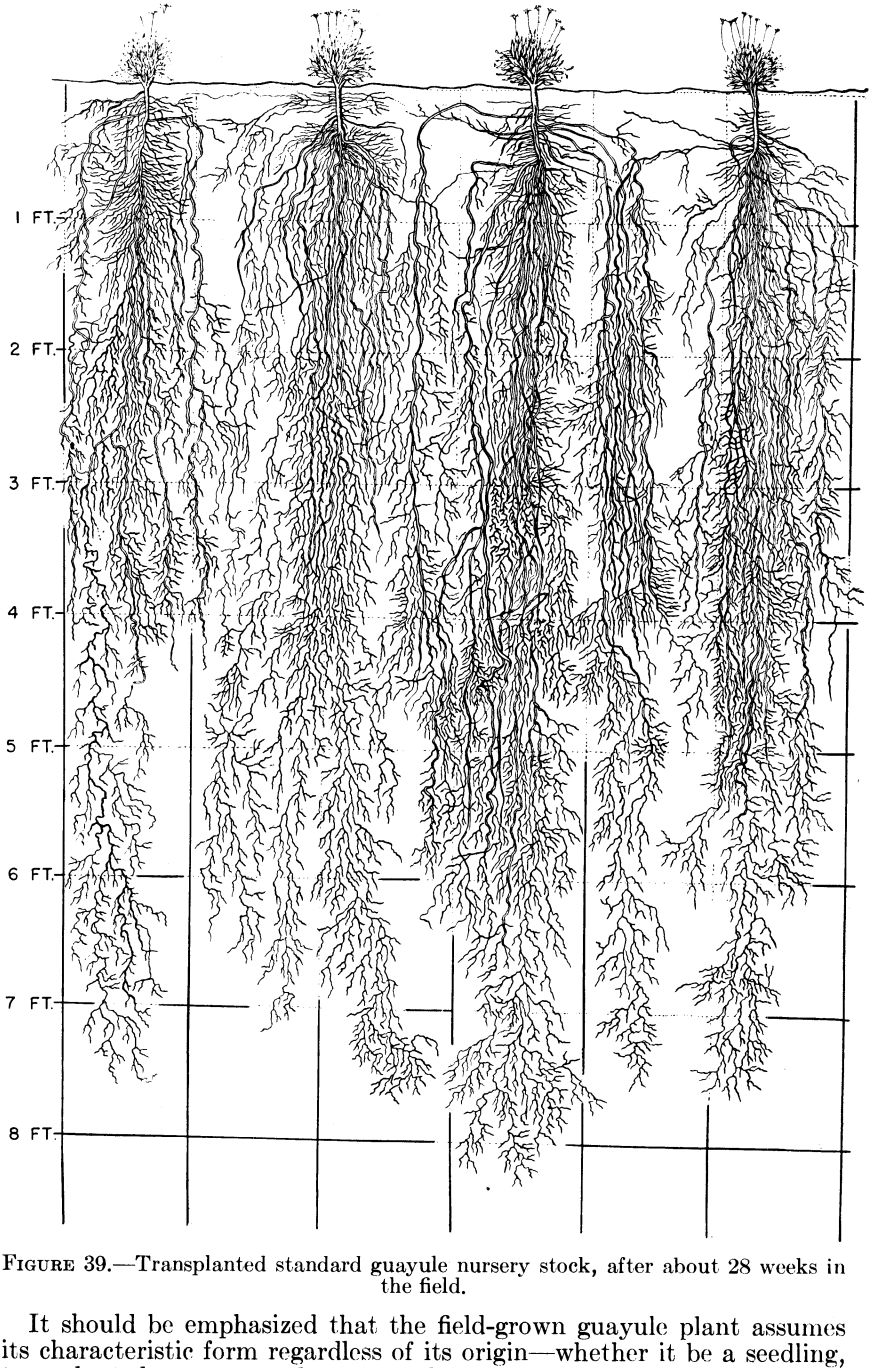

FIGURE 39.—Transplanted standard guayule nursery stock, after about 28 weeks in the field.

It should be emphasized that the field-grown guayule plant assumes its characteristic form regardless of its origin—whether it be a seedling, transplanted nursery stock, or rooted stem cutting. Only minor charac-

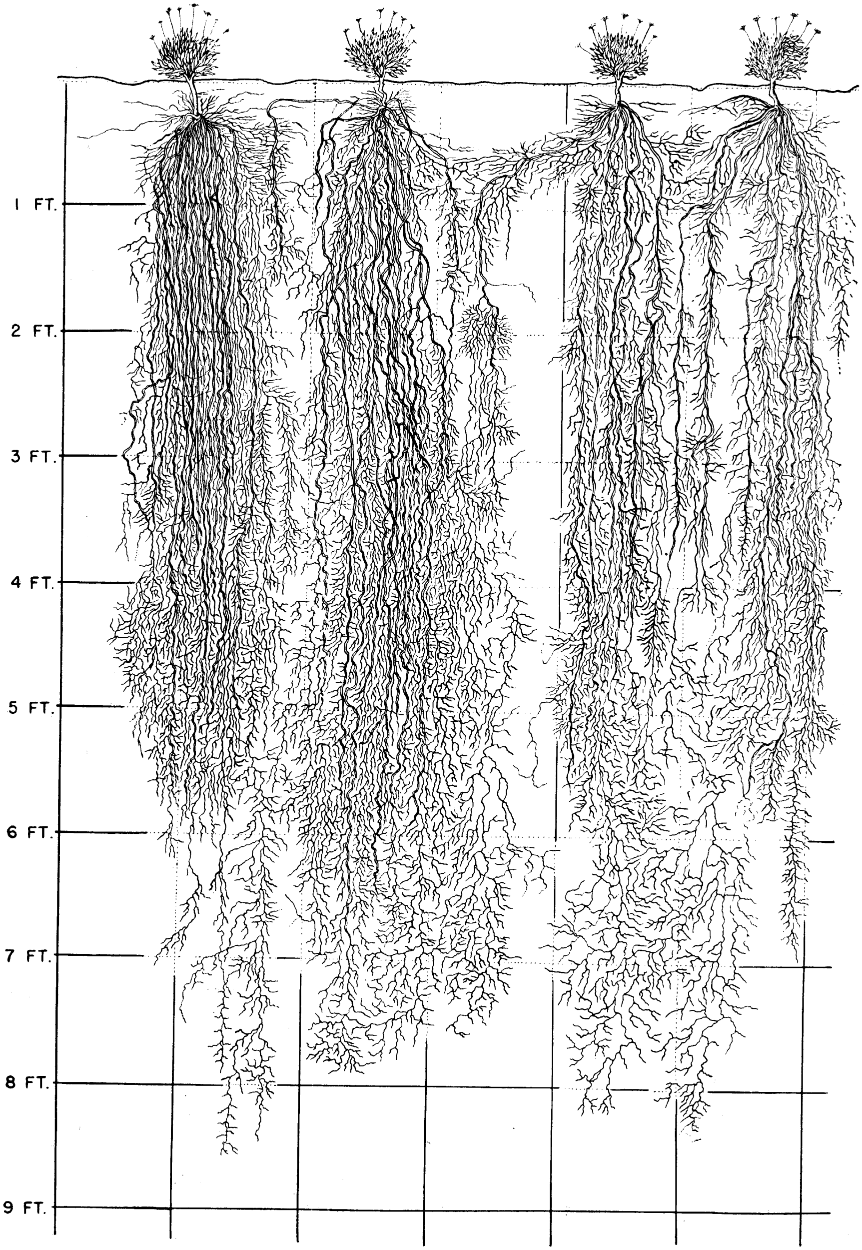

FIGURE 40.—Transplanted stem cuttings of guayule that had been rooted in the greenhouse, after about 28 weeks in the field.

teristics of form persist past the early periods of development; and these, insofar as a single season's growth is indicative, are eventually obscured.

Root Development of Nursery-Grown Plants

There is no reason why development of seedling roots in the nursery should differ appreciably from the same process in the field, especially in irrigated localities. In fact, from the standpoint of root development, furrow-irrigated nursery plantings would produce as good planting stock as the much more expensive overhead-irrigated plantings customarily made. The only difference in culture is the method of irrigation; overhead irrigation is applied at much more frequent intervals in the nursery than is furrow irrigation in the field.

To avoid repetition of illustrations, reference is made in this section only to drawings reproduced in other parts of the bulletin. Keeping in mind the 8- and 10-week-old plants shown in figures 25 and 26, note the 16-week-old plants shown in figures 76 (p. 87) and 77 (p. 88). The 16-week-old plants were grown in the nursery under conditions fairly similar to the field treatment of the 10-week-old plants. The nursery planting differed in having had overhead irrigation rather than furrow irrigation, in not having been thinned, and in being considerably older. Compare also the root development of the plants shown in figure 79 (p. 92). These seedlings were 14 weeks old, had not been thinned, and had grown under some degree of drought stress in the nursery. Although they were a month older than the plants shown in figure 26, their development was not a great deal more advanced.

Effects of Soil Factors on Root Response

It is difficult in many cases to distinguish between the chemical and physical factors of soil that may be influencing root responses to soil variation. In some instances it has been impossible to demonstrate conclusively whether a positive growth reaction resulted from greater moisture content or greater nutrient supply. It is likely that some such responses are due to a combination of the two conditions. Frequently, sandy soils with low water-holding capacity are also relatively sterile and soils of greater water-holding capacity are apt to contain a greater source of mineral nutrients. If, for the sake of clearness, one factor is discussed with apparent lack of regard for the other, it is not intended that the probable interrelation be dismissed.

SOIL TEXTURE AND NUTRIENTS IN RELATION TO ROOT DEVELOPMENT

Soil texture and structure influence simultaneously the moisture supply, penetrability to water, and penetrability to roots and through these the specific form that a root system will assume. The favorable soil type in which normal root development occurs has been described previously as having considerable depth, fair drainage, good aeration, penetrability, favorable fertility, and moderate water-holding capacity. With the exception of the remote relation of fertility, these are all resultant of soil structure and textural influence. Structure, independent to a large extent of both moisture and fertility, is influential in determining the degree of penetrability to roots and the efficiency of aeration.

Particular attention has been paid to the classification of the soils in which root excavations were made. The type and series of each were determined by the aid of maps prepared by the staff of the Division of Surveys and Operational Investigations, Emergency Rubber Project, United States Forest Service, and upon request specific studies of certain sites were made by some of these men. The maps on which determinations were based were drawn to the scale of 8 inches to the mile and carried considerably more detail than ordinary soil-survey reports. In most cases the types were checked by duplicate mechanical analyses of all recognizable horizons, and these analyses were further used as the basis of correlation of root behavior with soil variation.

The kind of soil variation to which the root systems responded was not always the difference on which types and series were based. Only rarely does a given soil type possess a textural feature of such constant character that there is a constant root response to it. Thus, Bryant loam is characterized by a claypan in several of its phases, but the degree of development of the claypan, its depth, and its effect on root growth in most instances vary more within one phase than they do between two related ones. Correlation with soil type, therefore, has yielded only a general picture of the textural soil features influencing root habit. A much closer correlation exists between root habit and determinations of moisture equivalents and mechanical compositions of specific horizons of each soil; such data have been used freely in evaluating soil factors, but their cumbersome nature prohibits their publication except in special cases where they are particularly required. Except in the most extreme cases, differences between series and types showed less corresponding differences in root habit than vertical variations in the horizons of single soil types.

SANDS OF VARIOUS KINDS

Sand differs from the favorable soil type in occasionally occurring as extremely light soil with very low water-holding capacity and probably low nutrient content. In this form it was encountered in the Salinas Valley, Calif., in the Coachella Valley at Dry Camp and at Whittier nursery, both near Indio, Calif., and on Yuma Mesa, near Yuma, Ariz.

In an irrigation experiment [5] set up on very light variants of Hanford loamy coarse sand in the Salinas Valley, root excavations revealed a striking response to a coarse sandy subsoil. The depth of favorable loamy surface soil overlying the relatively pure sand varied progressively from 13 to 36 inches. The next deeper horizon was a brownish transition about 24 inches in thickness between the loamy sand and a yellow coarse sandy subsoil. The soil was very porous, and leaching was undoubtedly favored. Nursery beds were sown May 9, 1944, and excavations of four sites were made September 15 and 16, 1944. The habitat conditions and the growth responses on the several sites are summarized in table 1.

In figure 41 are illustrated the plants from site A. Note that the dense root systems stopped abruptly at a depth of about 24 inches and that their development was by no means proportionate with the luxuriant top growth. The depth at which these roots were stopped is about halfway through the transition zone from loamy to coarse sand. Compare this with development shown by the plants from site B (fig. 42). The root systems here reached about 36 inches, or about the lower limit of the loamy sand layer. Although this planting was not nearly so heavily fertilized as that on site A, its top growth was equally luxuriant and its root penetration greater. There was a strong correlation between depth of loamy sand and penetration of roots.

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[5] Designed by L. C. Erickson, Special Guayule Research Project.

TABLE 1.—*Habitat conditions and growth response of guayule sown May 9, 1944, and excavated September 15 and 16, Salinas Valley, Calif.*

Site	Irrigation	Fertilizer	Depth of loamy surface soil	Moisture condition at time of excavation	Root depth	Aerial part of plant	
						Height	Growth condition
			Inches		*Inches*	*Inches*	
A....	0.25 in. twice weekly; increased to 0.5 in. by August 2; thereafter constant.	Heavy prior to sowing; nitrogen supplement August 2.	13	Unirrigated for 4 days; dry in upper 18 in.; very moist below.	24	8.5	Lush.
B....	...do.............	None prior to sowing; nitrogen supplement August 2.	36	Just irrigated; moist throughout.	36	9	Do.
C....	0.25 in. twice weekly until mid-July; thereafter dry.	None..........	14	Dry in upper 18 in.; very moist below.	20	2	Severely hardened.
D....	...do.............	Heavy prior to sowing; no supplementary nitrogen.	36	Dry in upper 24 in.; very moist below.	40	2.5	Do.

In figure 43 are shown the plants from site C. Here, too, the root penetration was stopped within the transition between loamy and coarse sands. Although the protracted drought period experienced by these plants had markedly reduced their top growth, their root development

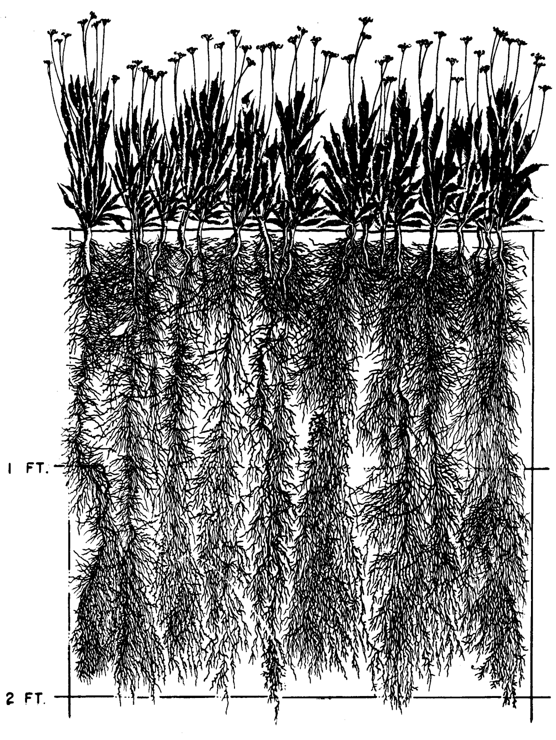

FIGURE 41.—Well-fertilized 4-month-old nursery plants of guayule grown under heavy irrigation in Hanford loamy coarse sand. The favorable loamy surface layer was only 13 inches deep here.

was comparable with that in plants from site A (fig. 41). Compare this with that of plants from site D (fig. 44). Although top growth in those from site D was slightly superior to that in those on site C, it did not compare with the luxuriant growth of those on sites A and B. Root penetration on site D, on the other hand, was better than that on the other sites and was closely correlated with the depth of the loamy sand layer.

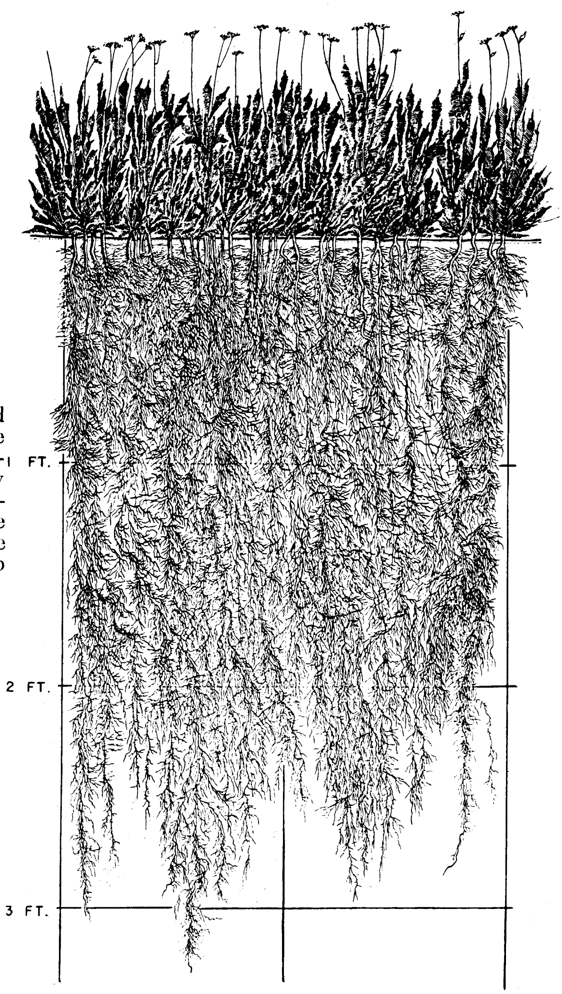

Figure 42.—Four-month-old nursery plants of guayule grown under heavy irrigation in Hanford loamy coarse sand but not fertilized prior to sowing. The favorable loamy surface layer was 36 inches deep here.

In this experiment top growth was correlated closely with abundance of moisture in the surface soil. Both of the continuously irrigated sites (A and B), regardless of fertilization or depth of favorable soil, produced luxuriant plants; both of the dry sites (C and D) produced only stunted plants in spite of the fertilization and greater depth of favorable soil on site D. Root penetration throughout was correlated with depth of favor-

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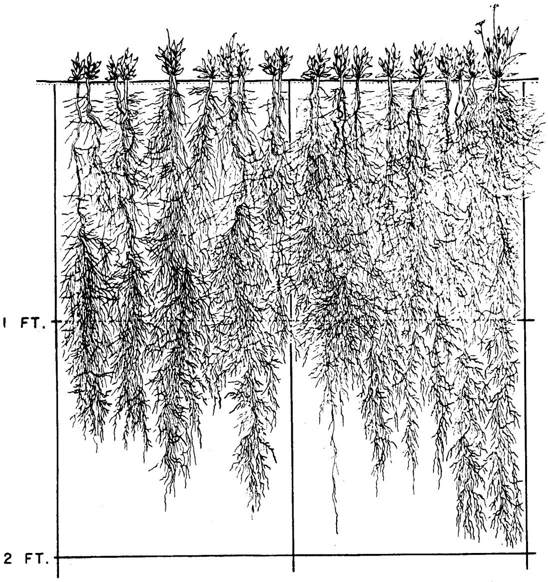

FIGURE 43.—Unfertilized 4-month-old nursery plants of guayule grown under drought stress since early ecesis in Hanford loamy coarse sand. The favorable loamy surface layer was only 14 inches deep here.

able loamy soil, no roots penetrating more than halfway through the transition zone between loamy and coarse sands. The application of fertilizer to sites A and D, both subjected to abundant early irrigation, resulted in no increased root penetration. The perceptible wetness of the subsoil definitely ruled out lack of moisture as the cause of limited root penetration even in the plots from which water was withheld. Yet, total penetration in no case equalled that of similar-aged plants in more favorable soils. (See, e. g., figs. 75–77.) Although sand, because of its poor water-holding capacity, has been shown to be detrimental to root growth, the much more xeric dune sand in the Coachella Valley described on page 53 showed no such marked effect as here observed. A possible high degree of sterility should be investigated.

At Yuma Mesa the soil is Superstition sand. A series of experimental plots[6] were planted to nursery stock on February 17, 1943. Root excavations of the 1-year-old transplants were made between February 16 and 19, 1944. All the plots showed much greater internal variability than the differences between plots. For instance, there was very little difference between one heavily fertilized plot and an unfertilized control plot, but within each about half the plants were distinctly stunted and the remainder nearly normal for their age.

In figure 45 are illustrated the larger plants from the heavily fertilized plot, and in figure 46 are shown stunted ones growing immediately adjacent. A similar series from the unfertilized control plot (figs. 47 and 48) can be compared with these. It is clear that the stunted plants had developed poor and sparse root systems regardless of fertilizer. It will be noted in figure 48 that the plant on the right had grown skewed to the left. This skewness had apparently resulted from competition with a large plant to the right.

[6] Designed by C. H. Davis, Special Guayule Research Project.

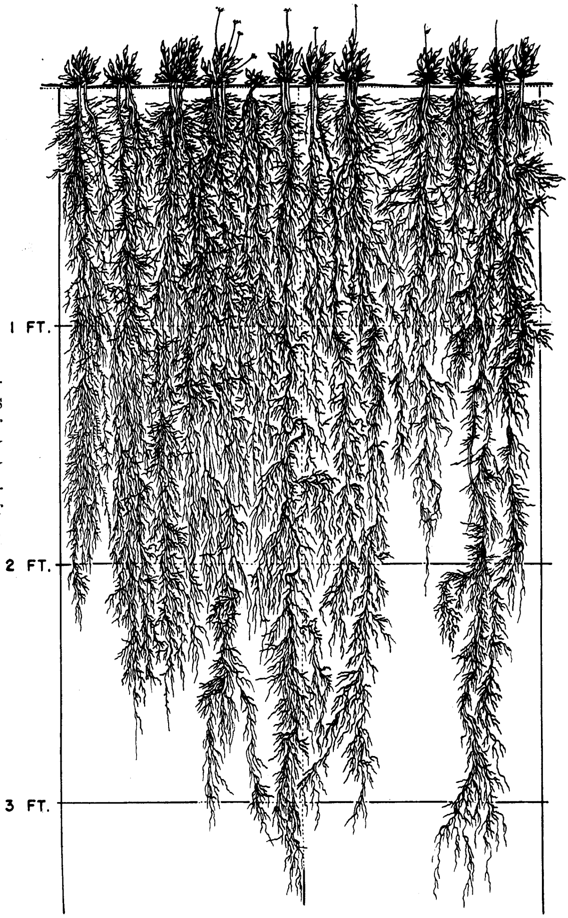

FIGURE 44.—Fertilized 4-month-old nursery plants of guayule grown under drought stress since early ecesis in Hanford loamy coarse sand. The favorable loamy surface layer was 36 inches deep here.

The very deep penetration of one root in figure 45 furnished what seemed to be a clue to the cause of the irregularity when it was noted that this root was following an old root channel containing some washed-in clay and a quantity of rotting plant remains. This was further corroborated by the excavation of a particularly large plant in a third plot (fig. 49). This plant owed its size partly to lack of competition and partly to the presence of much rotting plant debris in the soil. The land had been cleared of desert shrubs about a month before planting. The roots of the plant in figure 49 grew densely matted about the rotting roots of *Larrea tridentata*. However, a reexamination of the soil surrounding the plants in the first two plots revealed no appreciable consistent difference in the amounts of debris beneath stunted and normal plants.

It could be concluded only that minor local differences in water-holding capacity (as illustrated in extreme by the old root channel and the plant debris) had so affected the moisture relations of some individuals that they had resumed growth more promptly after transplanting and had maintained a more rapid rate of growth than their stunted neighbors in

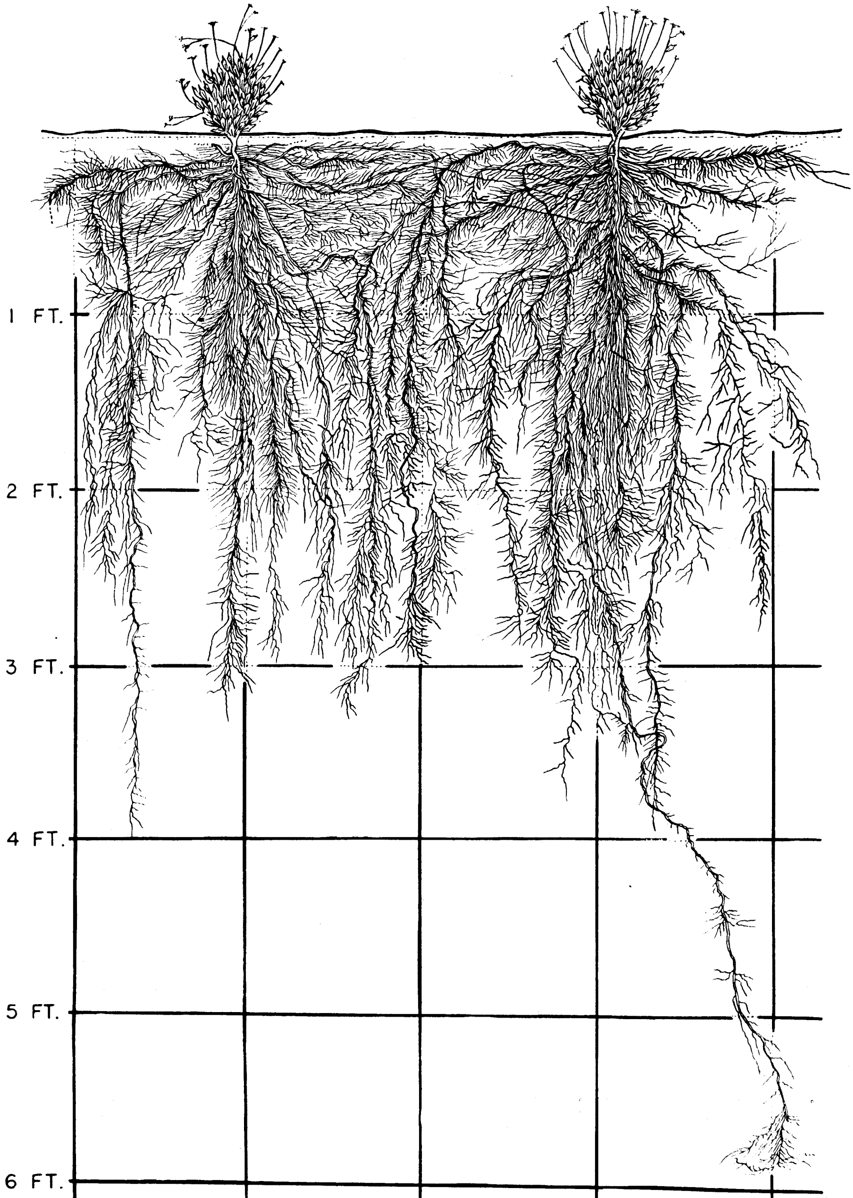

FIGURE 45.—Larger 1-year-old guayule transplants in heavily fertilized Superstition sand at Yuma Mesa, Ariz.

the unaltered sand with low water-holding capacity. That this effect was marked is illustrated by the fact that heavy application of fertilizers produced no appreciable response. The well-known requirement of moisture for the full utilization of nutrients seems again to be corroborated by the observations herein described.

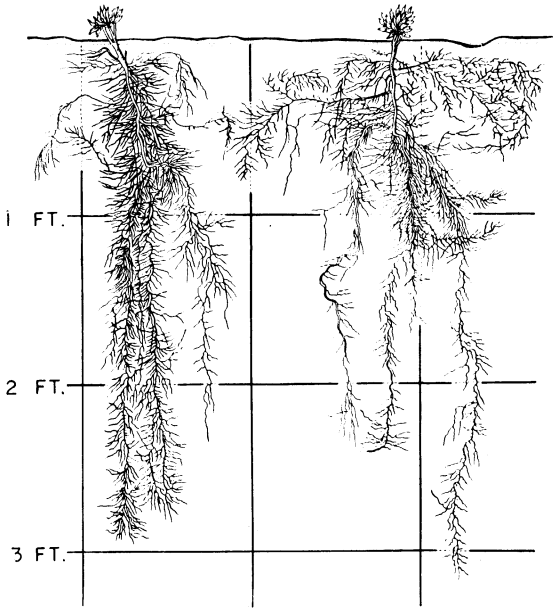

FIGURE 46.—Stunted 1-year-old guayule transplants in heavily fertilized Superstition sand at Yuma Mesa, Ariz. Note the poor development of both roots and tops as compared with those of figure 45 growing immediately adjacent.

The differential moisture relations of this soil were proved by field capacity determinations [7] on samples of the soil beneath stunted and normal plants in the Yuma Mesa plots. It was consistently found that the soil beneath stunted plants had a slightly lower field capacity than that beneath normal plants. That moisture is frequently critical in determining promptness of growth resumption of guayule upon transplanting has been demonstrated; sprouting is inhibited if the moisture content of the plant tissues falls below a certain critical percentage (7).

Near Indio a nursery planting in Indio very fine sandy loam was excavated February 1, 1944, at an age of 14 months. In figure 50 is illustrated the very irregular root habit of these plants. This irregularity was correlated with perceptible variations in the sandy soil, a condition more clearly illustrated by the results obtained at Dry Camp (p. 55). Beneath the second plant from the left may be seen a clublike mass of roots ending abruptly, which is shown in detail in figure 51. This rope of roots originated as a few simple principal roots that branched repeatedly, but the branches never succeeded in leaving the parental mass. The entire group was growing in a very nearly pure dune sand that retained very little water and was quickly dried after irrigation. As a branch left the ropelike mass of roots, it grew only a short distance laterally before some condition of the adjacent sand influenced it to rejoin the parental group. It is very likely that lack of moisture was the condition responsible.

CLAY HORIZONS

The most obvious manifestations of the effects of clay on root pattern are to be seen when clay alternates with nearly pure sand. The reactions

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[7] Made by C. H. Davis, Special Guayule Research Project.

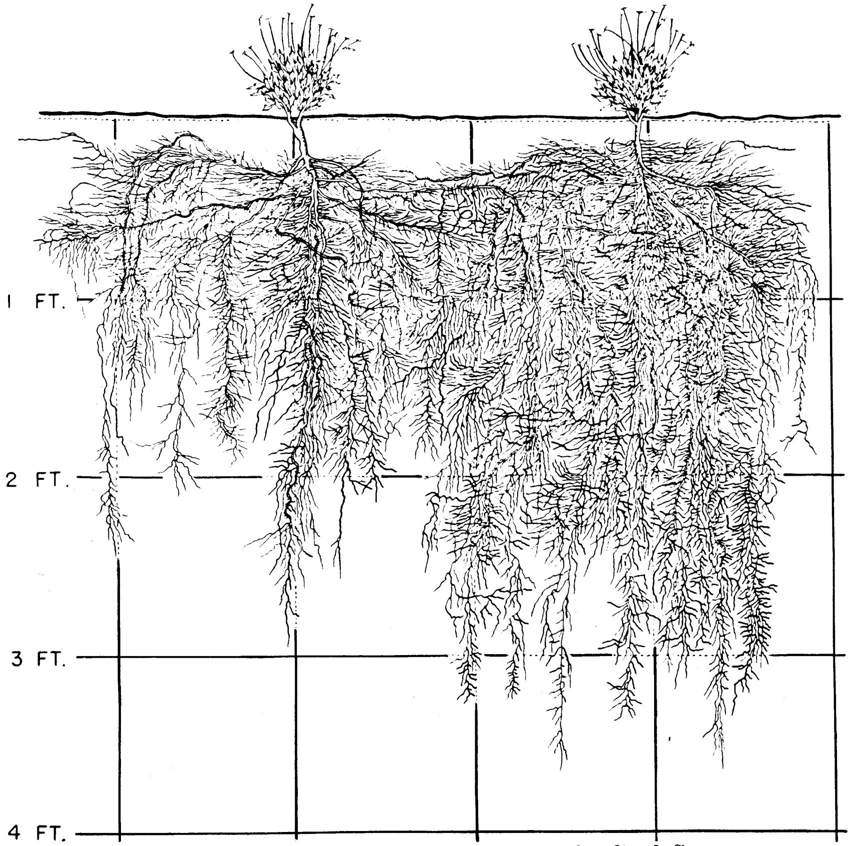

FIGURE 47.—Larger 1-year-old guayule transplants in unfertilized Superstition sand at Yuma Mesa, Ariz. (Compare with fig. 45.)

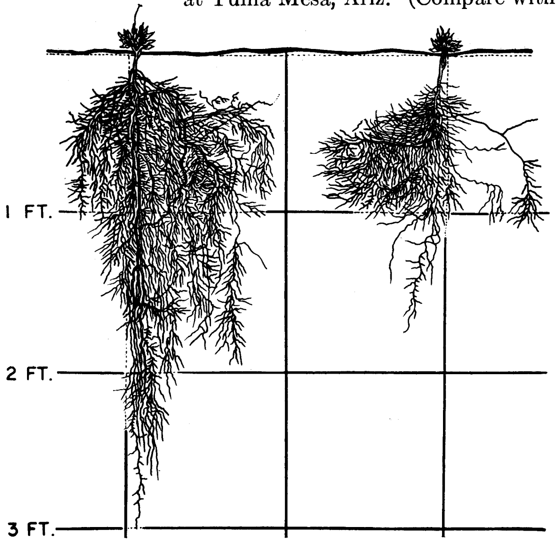

FIGURE 48.—Stunted 1-year-old guayule transplants in unfertilized Superstition sand at Yuma Mesa, Ariz., growing adjacent to the plants of figure 47. (Compare with fig. 46.)

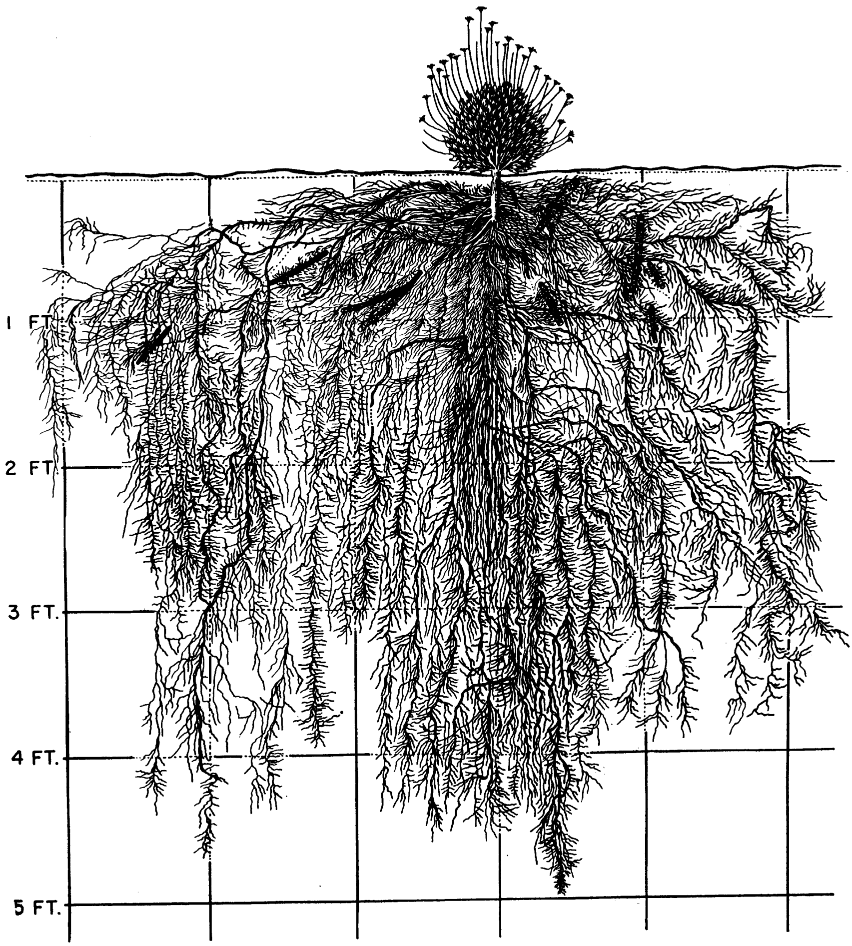

FIGURE 49.—One-year-old guayule plant in Superstition sand at Yuma Mesa, Ariz. Note the matting of roots about the decaying residue of recently killed *Larrea tridentata.* The wide spread of lateral roots resulted from lack of close neighbors.

of the roots here explain similar but less pronounced variations where the vertical components of the soil profile show less contrast.

The sharpest distinctions between immediately adjacent volumes of soil encountered in this study occurred at Dry Camp. The soil there, Coachella loamy sand, is of dune origin. It consists of a matrix of nearly pure sand, analyzed as 96 percent sand and 4 percent silt and clay. Buried in this matrix at various levels are broken horizontal veins of nearly pure silty clay. These veins contain 2 percent sand and 98 percent silt and clay; of the total, 22 percent proved to be colloids. The moisture equivalent of the sand was measured at 1.5 percent, while that of the silty clay equalled 43 percent. The form of the broken veins (fig. 52) is that of silt deposits subsequently dried and cracked into polygonal blocks or chips that so frequently occur along river flood plains. The blocks

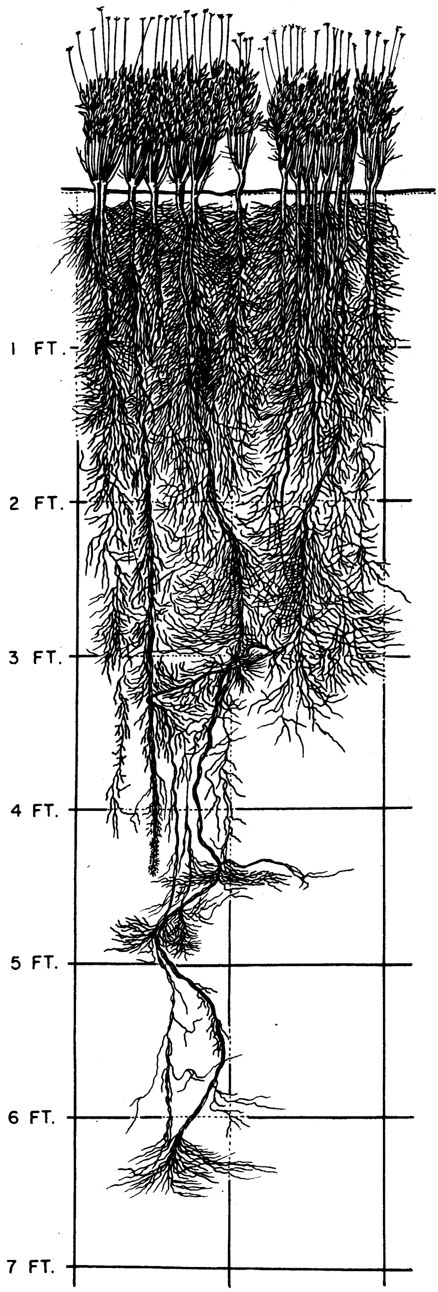

FIGURE 50.—Fourteen-month-old nursery plants of guayule in Indio very fine sandy loam at Whittier nursery, near Indio, Calif. Note the irregular root distribution and the "rope" of roots on the left in the fifth foot in a horizon of nearly pure sand.

comprising these broken veins are concave on their upper sides, and their edges are sharply broken. The spaces between them are relatively narrow and are filled with sand. The thinner veins may be unbroken and

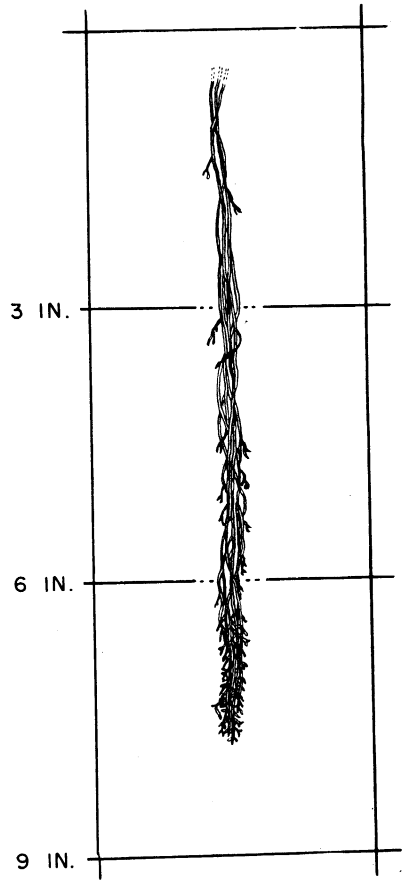

FIGURE 51.—A mass of roots in a horizon of nearly pure sand in the fifth foot of Indio very fine sandy loam (larger scale drawing of the "rope" shown in fig. 50). Note the numerous branches that failed to leave the parent roots.

are apt to be of relatively small extent.

Cultivation and other disturbances have rather efficiently mixed the clay and sand of the surface foot to form a loamy sand consisting of about 64 percent sand, 19 percent silt, and 17 percent clay. Of the total, about 6.5 percent is colloids. The moisture equivalent of this surface soil was determined to be about 12 percent. The presence of clay is responsible for a large share of the water-holding capacity of the soil in this area.

That the alternation of clay layers and sand is a widespread phenomenon in the Coachella Valley is evidenced by its occurrence both north and south of Indio. Four widely separated excavations were made at Dry Camp, and the condition was observed in each.

The effect of the localized clay on the distribution of roots is clearly shown in figure 53. These plants were grown in nursery beds in Coachella loamy sand under conditions of standard practice. They were 7 months old when excavated on January 18, 1944. The soil had been fertilized at the rate of 60 pounds of nitrogen, 120 pounds of phosphate, and 100 pounds of potassium per acre prior to planting. Subsequently 20 pounds of nitrogen per acre was applied as a side dressing. The top soil was quite pervious, and the leachable minerals should have been carried

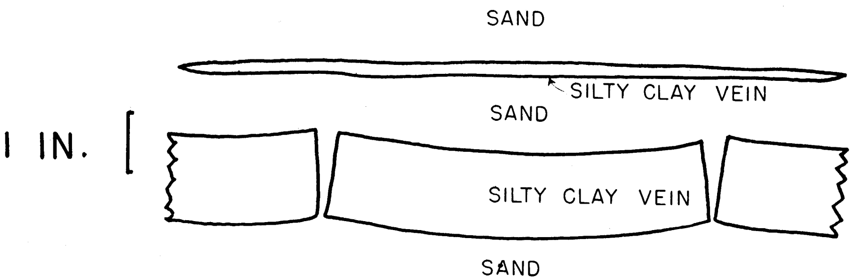

FIGURE 52.—Silty clay veins in nearly pure dune sand occurring at various horizons in Coachella loamy sand. Note the resemblance of the thicker layers to the cracked silt layers of flood plains.

through the profile by the moderate weekly irrigations from June until October.

The surface foot of loam soil was fully occupied by roots, which became progressively more sparse as the pure sand was entered (fig. 53). The strong horizontal disposition of feeder branches is evident at 24 and 52 inches below the surface. These corresponded to the position of clay veins. The less pronounced tendency to branch horizontally at 60 inches was caused by the roots just having entered another clay vein at that depth. The dense accumulation of principal roots to the right was induced by the presence of an old alfalfa root channel in which organic debris and washed-in clay presented more favorable moisture and nutrient conditions.

The marked response of the roots upon reaching a piece of buried clay would not have been caused by nutrients alone. Rather, it appears likely that the more favorable moisture relations offered by the clay were responsible for normal mineral absorption in the clay and that lack of moisture in the sand was the limiting factor there.

Figure 54 illustrates in detail the responses of roots to the presence of the clay. The ropelike mass of roots at the left, similar to the one described previously, proliferated broadly upon entering the clay layer. A single root at the right reacted similarly. The downward growth past the clay zone was not nearly so pronounced as lateral growth within the clay. In both cases the production of lateral branches was favored even above the level of the clay layer, apparently by the close proximity of a large water supply in the clay which kept the immediately adjacent sand moist.

An experiment was designed to determine the effect of soil texture on root habit in the greenhouse. Gallon cans were prepared containing relatively sterile fine gravel and sand with a 1-inch layer at middepth consisting of diatomaceous earth of highly nonadsorptive nature. The gravel and sand mixture had previously been tested extensively and found to be very deficient in nutrients; it supported root growth of guayule, but top growth required the addition of mineral nutrients. Chemical tests of the diatomaceous earth for the presence of nitrates, phosphates, chlorides, and sulfates were entirely negative. The substratum, then, was nutritionally a relatively sterile system consisting of two layers of coarse material divided by a layer of fine material. The deficiency of nutrients in the coarse layers, the retarded top growth of the plants, and the nonadsorptive quality of the diatomaceous earth strongly indicated that there was no concentration of nutrients in the fine layer.

When the cans were wet, a small amount of the diatomaceous earth washed through and was lost, but the remainder formed a jellylike mass not unlike wet clay. Subsequent examination of the lower gravel layer

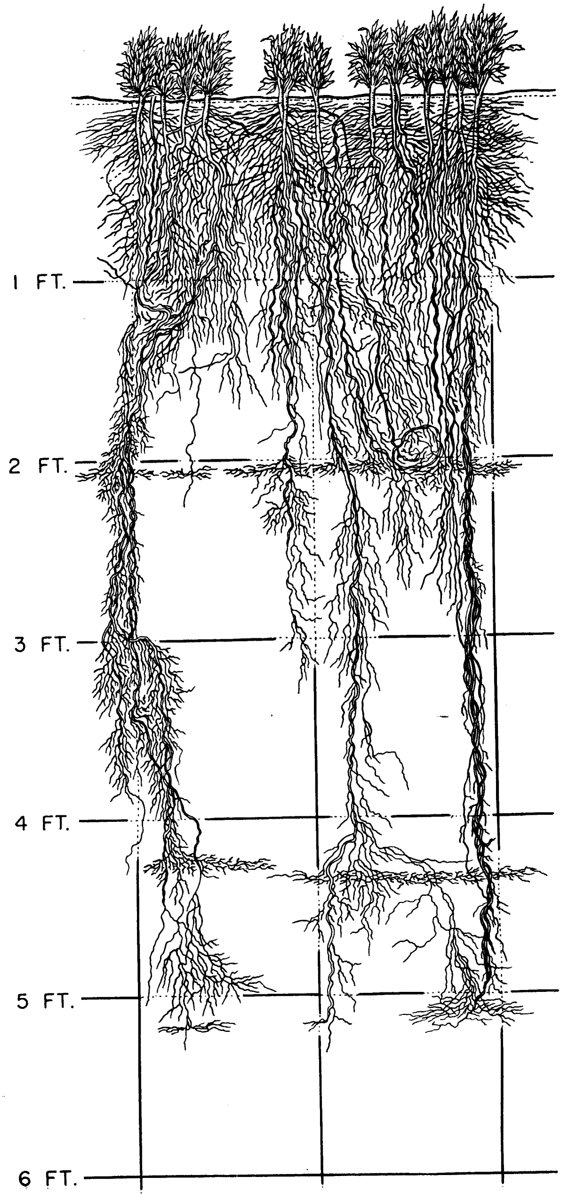

FIGURE 53.—Seven-month-old nursery plants of guayule in Coachella loamy sand near Indio, Calif. Note the concentrations of feeder roots in horizontal layers corresponding to veins of clay and silt and the aggregation of principal roots in an old root channel on the right.

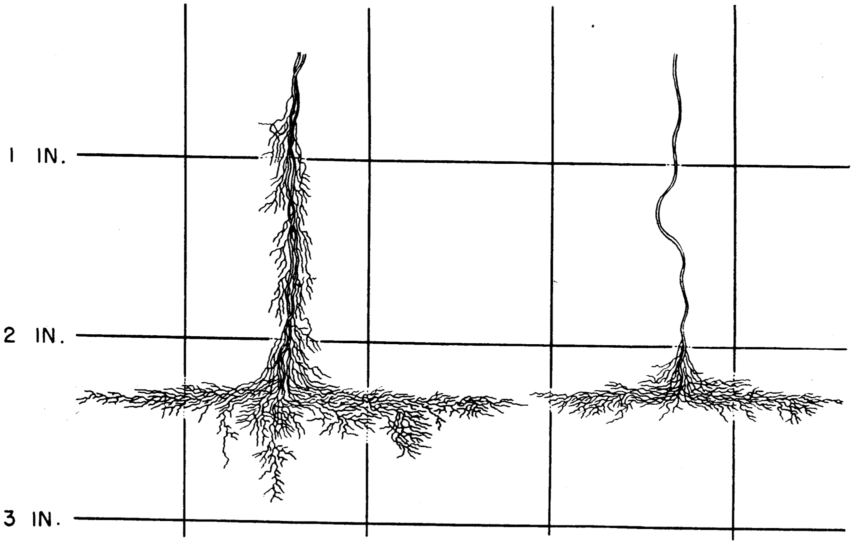

FIGURE 54.—Guayule roots passing from dune sand to clay veins. Note the absence of branches or their effective suppression in the sand and their ramification in the horizontal clay layer. (From the plants shown in fig. 53.)

showed it to be clean and free of any perceptible accumulation of diatomaceous earth. The bottoms of the cans were adequately drained.

In each of four cans thus prepared were planted three young guayule seedlings. Two cans were watered with distilled water and the other two with Hoagland's solution. Almost daily watering was required for the first month. At the end of 2.5 months the cans were split open and the contents were carefully examined with the aid of a fine jet of water. At this stage the roots had just reached the bottoms of the cans. In all four cans the roots followed the same pattern. In the upper gravel layer a few principal roots with sparse branches grew nearly straight down. Upon contact with the diatomaceous earth layer, these branched profusely and permeated the layer of fine material rather thoroughly. In the lower gravel layer the roots again became sparse and poorly branched.

Although the plants given one treatment received nutrient solution and those given the other remained relatively sterile, there was no corresponding difference in the ramification of the roots in the fine material. In fact, the plants in one of the sterile cans showed a slightly higher degree of root concentration in the fine material than did those in the cans to which nutrients had been added. It must be concluded, therefore, that the concentration of root branches in the fine material was due to causes other than the adsorption of nutrients there. The only remaining factor is that of soil-moisture availability. By virtue of its fineness, the diatomaceous earth simulated clay both in the amount of water it held and in the close contact it afforded the roots.

The situation in this experiment is entirely analogous to that of the clay veins included in dune sand in the profile of Coachella fine sandy loam (p. 55). The results here obtained add weight to the conclusion that root ramification in the clay veins was a response to moisture availability.

A greenhouse experiment designed for the study of the relation of soil moisture to nutrient absorption involved plants with their root systems divided by a waterproof partition in the culture chamber. The culture chambers were filled with sterile, repeatedly washed fine gravel and sand. Controls watered only with distilled water produced practically no top growth and only enough roots to permit the plants to survive. The plants given one treatment were consistently watered on one side with distilled water while the other half of the root system received Hoagland's solu-

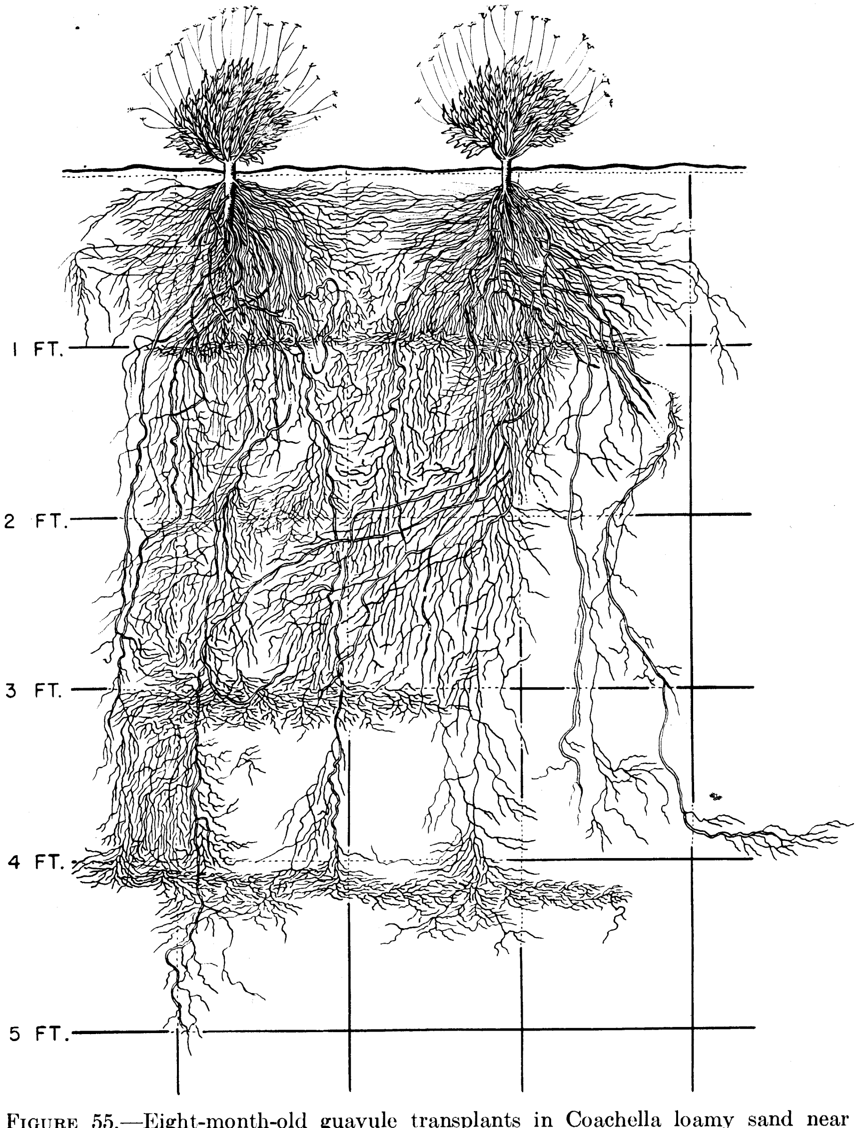

FIGURE 55.—Eight-month-old guayule transplants in Coachella loamy sand near Indio, Calif. Note the very irregular courses of the principal roots and the concentration of feeder roots in clay veins.

tion. The cultures were kept well watered, and the plants grew lushly. Upon being harvested the root system of each plant in this experiment was carefully examined. The two parts of each root system differed only in their bulk. The more numerous and heavier roots on the nutrient side formed a system about three times as large as that on the sterile side. The roots grown in an abundance of nutrients differed in no quality except size from those grown in very sterile sand. The number of principal roots, and therefore the bulk of the entire system, was greater on the nutrient side than on the sterile side. The appearance of the roots, the manner and frequency of branching, the length of branches, and the abundance of root hairs were the same under both conditions. It appeared that the roots on the sterile side had merely grown more slowly (as, indeed, repeated observation through inclined glass windows had shown them to be doing) and that the roots on the fertile side at an earlier and comparable stage of development would have been no different. At least, there was no reflection on the nutrient side of the profuse branching of roots growing in clay.

The plants shown in figure 55 were 8-month-old transplants grown in Coachella loamy sand. Note the very pronounced overlapping of lateral principal roots as well as the prominence of feeder branches in the clay veins. The thick vein at 3 feet did not extend fully across the excavation site.

The nursery plants shown in figure 56 were about 14 months old. Although the presence of prominent clay veins at 2-, 3-, and 5-foot levels was clearly reflected in the density of feeder branches, the advanced age of the plants had partially obscured the response by permitting time for the eventual rather strong development of branches in the sand. Furthermore, on this site the sand was not so pure as that on the sites described previously. In addition to numerous minor veins, some parts of the profile contained an appreciable quantity of clay mixed with the sand. The sand horizons were nevertheless sufficiently light so that the presence of an old alfalfa root channel on the right resulted in a considerable disparity of top growth. The large plants to the right all funneled into the old root channel, where the improved moisture and nutrient conditions favored their more rapid growth. It was noted that all parts of this nursery planting previously sown to alfalfa were characterized by scattered clumps of such large plants while the matrix of the stand consisted of stunted individuals like those at the left in figure 56.

No very satisfactory experiment has ever been devised to determine the effect of nutrient concentration in the field upon root habit, for it is exceedingly difficult to rule out the correlation of nutrient elements in the soil with moisture-holding capacity. Weaver (*18, p. 68*) concluded from the literature and his own observations that the greater frequency of branching in clay layers is the result of nutrient concentration as affected by moisture supply. Results obtained with guayule fully bear this out. It has been pointed out previously that in the Coachella Valley intensive branching occurred in clay lenses included in a sand matrix even though the soil had been heavily fertilized, and the same phenomenon was produced experimentally in nutritionally relatively sterile cultures. Furthermore, as described previously, the failure of guayule root branches to grow away from the parent root and into the dry sand rather clearly indicated that, whatever the nutrient situation might have been,

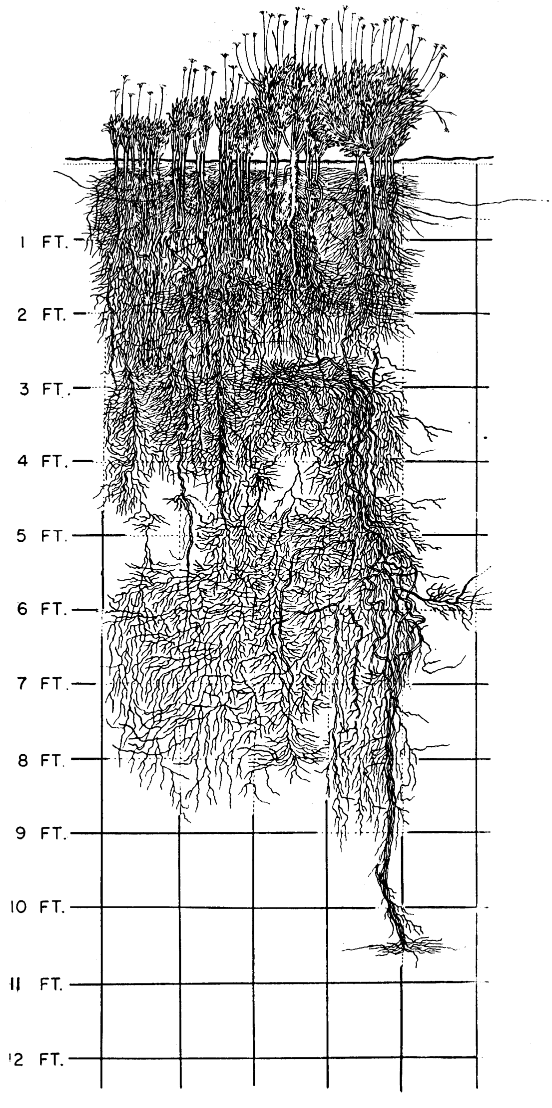

FIGURE 56.—Fourteen-month-old nursery plants of guayule in Coachella loamy sand near Indio, Calif. The sand here was adulterated by silt and clay, and the effect of clay veins was therefore reduced. Note, however, the concentration of principal roots in an old alfalfa root channel on the right and the superior growth of the plants affected.

lack of moisture was the limiting factor in this case. Excavations in adjacent unfertilized plantings revealed similar root responses to alternating sand and clay. Also, very heavily fertilized and unfertilized sand at Yuma Mesa showed no appreciable differences in plant growth or root habit. One is forced to conclude that where moisture and nutrients are both varied, moisture is the more definitely limiting factor because it also influences nutrient absorption.

The effects upon root physiognomy of clay as a concentration layer in a normal soil profile are often rather subtle, particularly if the upper soil horizons have a fairly high water-holding capacity and are not too markedly different from clay in that respect. In such instances the adjoining horizons are nearly as favorable to feeder concentration as the clay layer, and the dense ramification in the clay layer is then rather completely masked. In the process of root excavation the concentration of feeder branches in such a clay layer is sometimes more obvious to the excavator than to the artist. While loams are readily washed and one can see all the roots of the sample at one time, stiff clays wash poorly even with the mechanical aid of a pick; only a few roots are visible at a time and their density can be underestimated.

In figure 57 the vertical irregularity of roots was correlated with alternation of clay and sandy loam horizons in the profile. The plants were

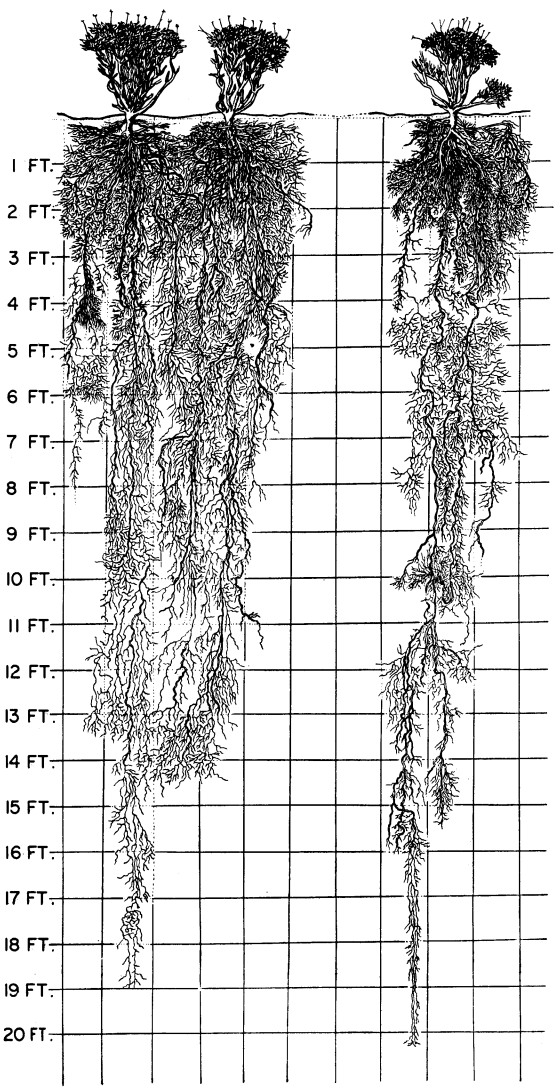

FIGURE 57.—Fourteen-year-old plants grown without irrigation in Greenfield coarse sandy loam overlying old Bryant horizons in the Salinas Valley, Calif. Note the concentrations of feeders in the claypan of the Bryant soil, especially between the 4- and the 6- to 7-foot levels.

about 14 years old and showed signs of deterioration. They were grown without irrigation in the Salinas Valley in a shallow phase of Greenfield coarse sandy loam overlying several old Bryant profiles, whence the clay

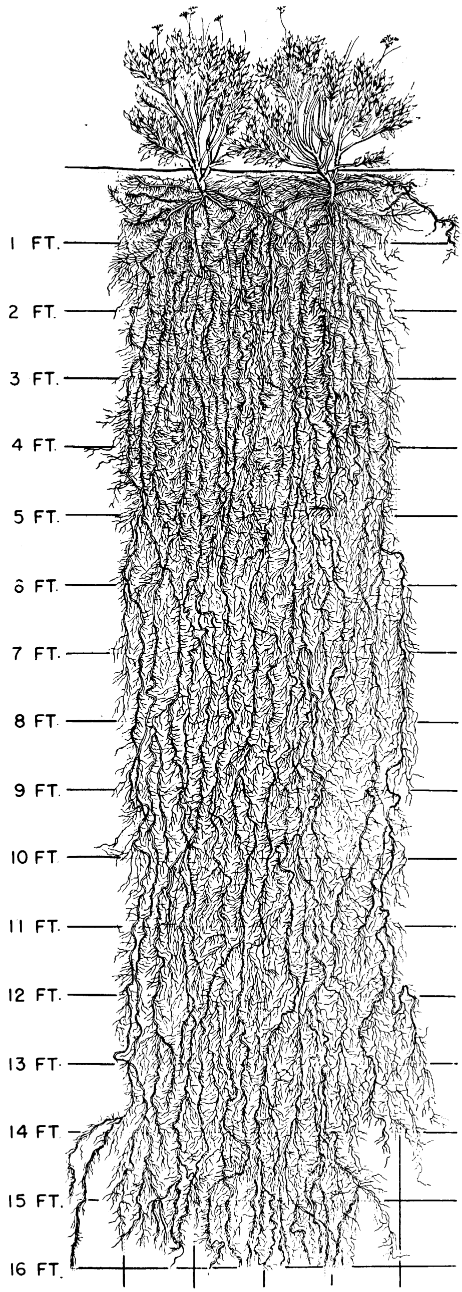

FIGURE 58.—Two-year-old guayule plants, spaced 24 inches within the row and grown without irrigation in Lewisville silty clay at San Antonio, Tex. Note the even distribution of feeders in the several horizons whose sharp differentiation involved essentially no change in moisture relations.

horizons. The sparseness of feeder roots between 3- and 4-foot levels corresponded to a horizon of light sandy loam of no great water-holding capacity. The concentration of feeders between 4- and 6- to 7-foot levels

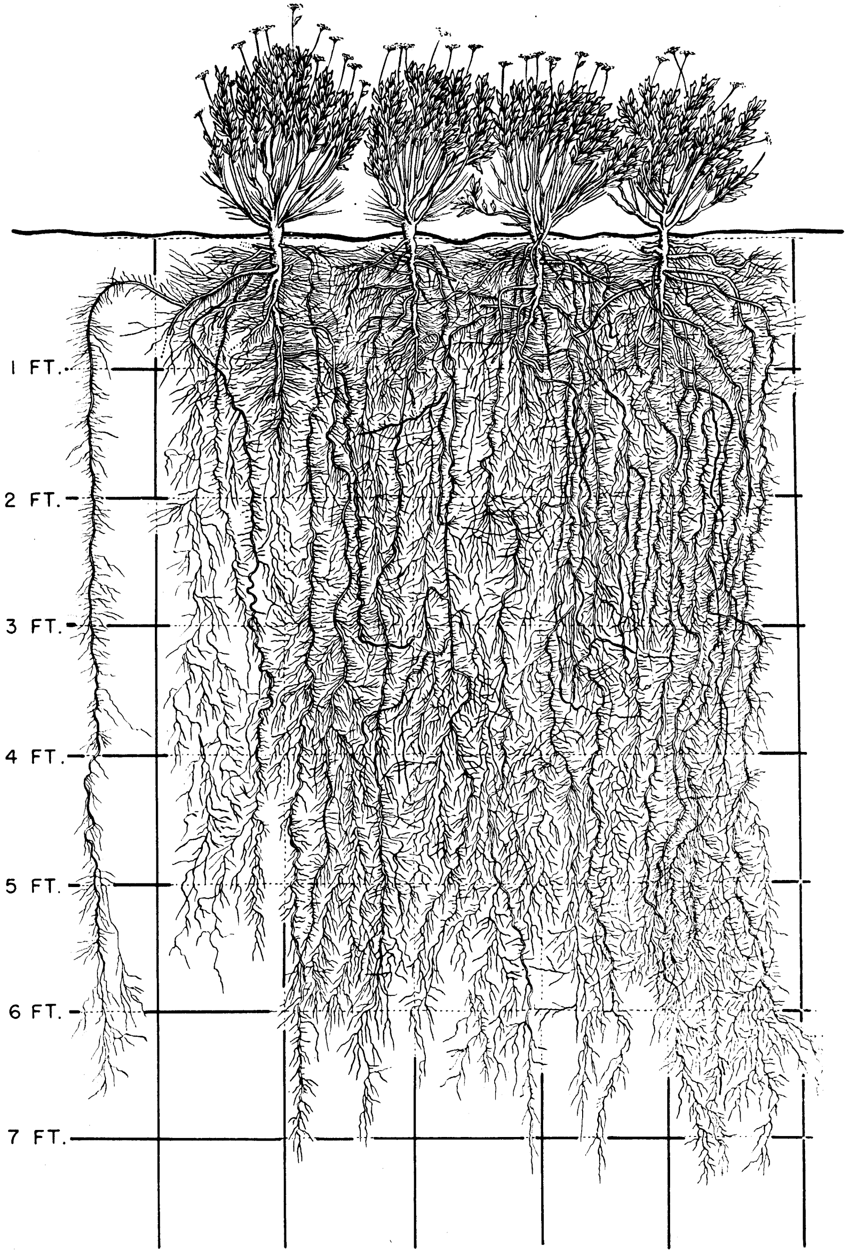

FIGURE 59.—Two-year-old guayule transplants grown under irrigation in Crystal fine sandy loam at Carrizo Springs, Tex.

was correlated with clay layers of variable thickness. Below 7 feet additional alternations of light- and heavy-textured soils were reflected accurately by the variations in density of roots, corresponding probably to varying supplies of both water and nutrients. There was also distinct evidence that waterlogging induced by the heavy clay layers had caused some root deterioration, thus augmenting the sparseness of roots in the light soils immediately above the dense clay horizons.

If there is no appreciable difference in nutrient concentration or in water relations among the several horizons of a soil, all types of concentration of soil components and differentiation of horizons result in no great response by roots. The Lewisville silty clay studied near San Antonio, Tex., was such a soil. The surface soil was a brownish-gray to a dusky-brown silty clay with a moisture equivalent of 25 percent. At a depth of 4 feet the soil was a light yellowish-brown silty clay with small aggregates of soft caliche and a moisture equivalent of 23 percent. At 8 feet a gray-mottled yellow clay of blocky structure with large caliche aggregates had a moisture equivalent of 27 percent. At 14 feet a gray-mottled yellow fine sandy clay had a moisture equivalent of 24 percent. Although the differentiation of horizons was very marked, the water relations of these materials, as indicated by the moisture-equivalent percentages, remained fairly constant at the various levels. This was reflected in the relatively even distribution of feeder roots in the 2-year-old plants excavated there about April 20, 1944 (fig. 58).

CLAYPANS

A very dense accumulation of clay at a relatively shallow depth forms what is termed a "claypan." Such a feature has a deleterious effect upon plant growth by resisting root penetration, retarding drainage, and causing poor aeration. Claypans form in various degrees of density, thickness, and depth with correspondingly variable interference with the movement of water and growth of roots.

At Carrizo Springs, Tex., Crystal fine sandy loam was found to have a minor layer of concentration consisting of yellow-brown or gray clay loam between 27 and 61 inches below the surface. The surface soil has a moisture equivalent of about 5 percent; at 42 inches and at 84 inches it is about 12 percent. Figure 59 shows 2-year-old transplants grown in this soil under irrigation. Note that there was no great differentiation of feeder concentration throughout the entire root system. Frequent irrigation had mitigated the droughty condition that would have been expected in a surface soil of such low moisture equivalent.

A fine-textured subsoil phase of Crystal fine sandy loam occurs immediately adjacent to this site. In it the surface 18 inches consists of fine sandy loam with a moisture equivalent of about 5 percent. Between 27 and 40 inches below the surface there is a dense claypan of blocky structure, brown in color and mottled with light gray. Between 40 and 58 inches below the surface occurs a columnar red clay. This material has a moisture equivalent of about 21 percent. The plants shown in figure 60 were grown on the claypan site under conditions otherwise equal to those described for the plants in figure 59. Note that the root distribution below 2 feet was very irregular and relatively sparse and that top growth in these plants was much inferior to that of the plants in figure 59. The density of the claypan, as revealed by the relatively high moisture equiva-

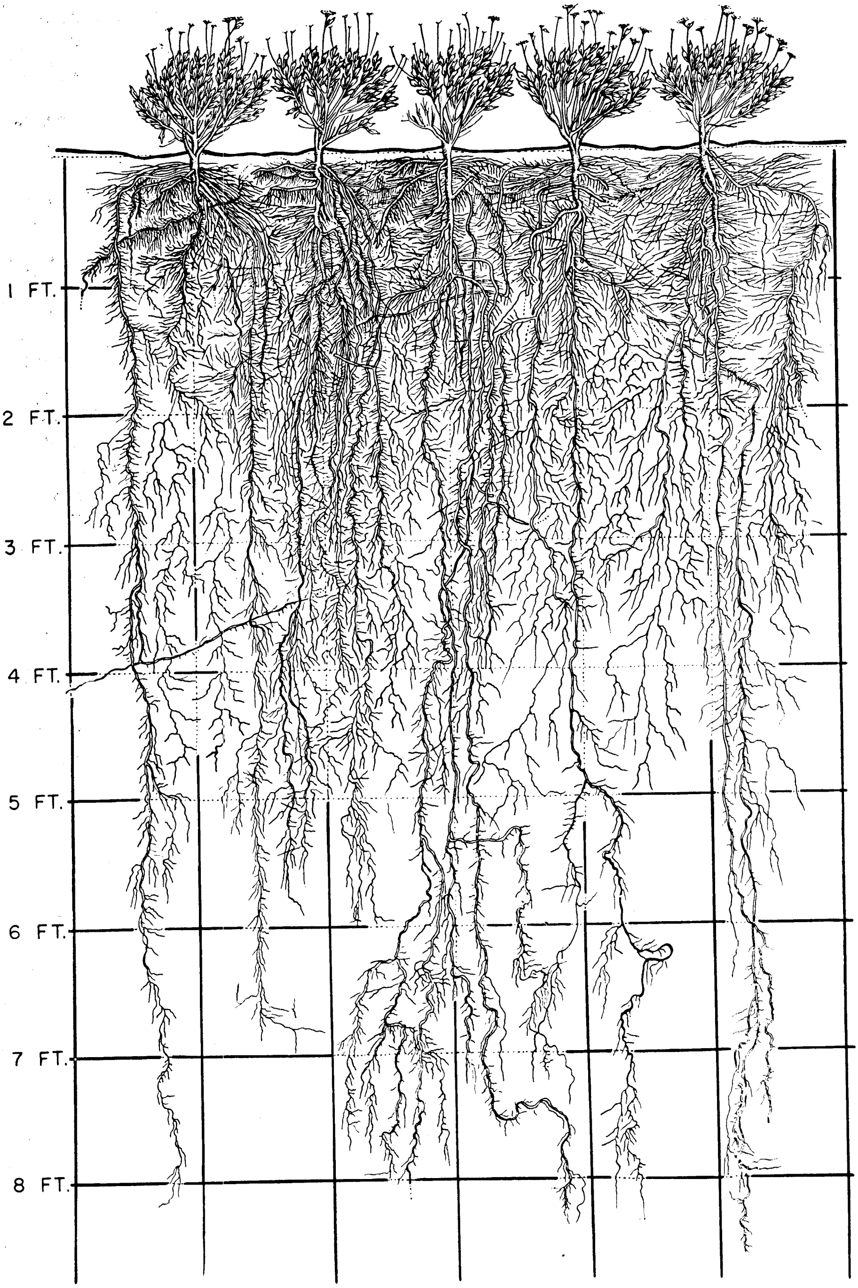

FIGURE 60.—Two-year-old guayule plants grown under irrigation in Crystal fine sandy loam, fine-textured subsoil phase, at Carrizo Springs, Tex. A dense claypan below 24 inches was frequently waterlogged and caused the loss of many principal roots and the ragged appearance of the root systems.

lent at about 40 inches, was sufficient to retard the drainage. This manifested itself not only in the mottled color of the upper clay layer but also in the presence of a number of dead guayule roots. These necroses produced the irregularities that characterize the root systems in this soil. Whether death was directly the result of waterlogging or the conditions of the waterlogged claypan favored diseases was not clear in the evidence observed. It was obvious, however, that no such ill effects occurred in either of two excavations in soil free of dense claypan, of which figure 59 represents one.

Much more severe claypan was observed in Bryant loam, mottled subsoil phase, in the Salinas Valley. This soil consisted of 15 inches of light-brown loam of moderately permeable nature lying on a heavy, yellowish-brown to dark-red columnar claypan between 15 and 52 inches below the surface. Below the claypan there was a permeable yellow gravelly clay subsoil. Very little mottling of the upper claypan indicated

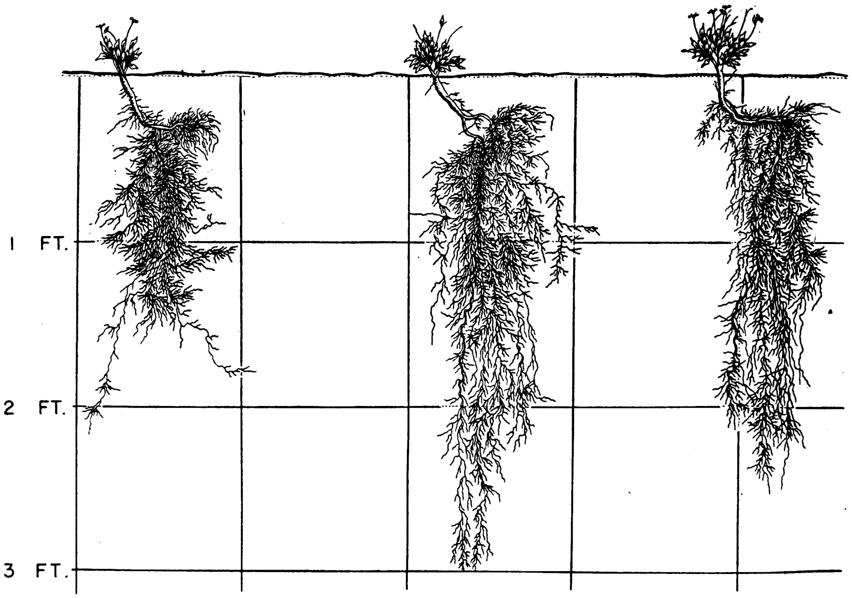

FIGURE 61.—Eight-month-old guayule transplants grown without irrigation in Bryant loam, mottled subsoil phase, in the Salinas Valley, Calif. A dense claypan lay between 15 and 52 inches below the surface. Note the irregular root systems and the poor top development.

that the slight slope was sufficient for fair drainage. Plants about 8 months old excavated about the end of August 1944 are shown in figure 61. Note the extreme stunting and sparse flowering of the tops and the very irregular root growth. It is significant, however, that some roots reached a depth of 36 inches, having passed through nearly two-thirds the thickness of the claypan. This site had recently been cleared of a stand of 14-year-old guayule which consisted of plants about 10 inches tall and 12 inches broad; a neighboring site of Greenfield coarse sandy loam produced plants 2 feet tall and nearly as broad (fig. 57). In the fissures of the columnar claypan dense nets of dead guayule feeder roots of the previous crop were visible even as deep as the bottom of the clay layer. It may be presumed that another growing season with adequate moisture would have permitted the penetration of the roots of the present crop to the more permeable subsoil.

Similarly, those plants of the present crop growing on deep Greenfield coarse sandy loam near the claypan site were developing more normally. In figure 62 are illustrated the more luxuriant and heavily blooming tops and the more regular and denser root systems of such plants. Penetration here is not much greater than in the claypan, but the root pattern is more even and therefore more efficient in occupying the soil. Since these plants were all grown without irrigation, the total growth does not compare favorably with that of much younger plants in irrigated fields. Note, for instance, the transplants in figure 38, 68 days after they were set out.

Another site in the Salinas Valley had Bryant loam with an even more effective claypan. Here the surface 10 inches comprised a moderately permeable layer of gray loam. Between 10 and 14 inches below the surface lay a sharply defined layer of yellowish-gray clay strongly discolored by waterlogging. From 14 to 25 inches the clay was dark red and columnar, and between 24 and 36 inches it was massive and yellowish red. Below 36 inches was a yellowish-brown gravelly loam subsoil. It is doubtful whether the claypan here was much more dense than that occupied by the plants in figure 61. However, the surface was nearly flat, and the site lay at the edge of a small hog wallow so that water accumulation was encouraged. Here, too, irrigation was lacking, but the

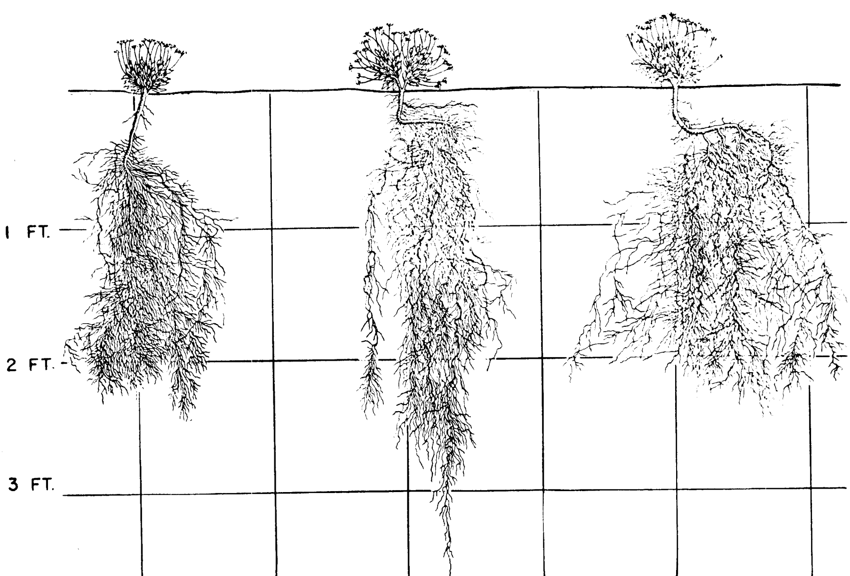

FIGURE 62.—Eight-month-old guayule transplants in Greenfield coarse sandy loam adjacent to the plants shown in figure 61. Note the more regular root systems in the absence of a claypan, their more complete occupation of the soil volume, and the superior top development.

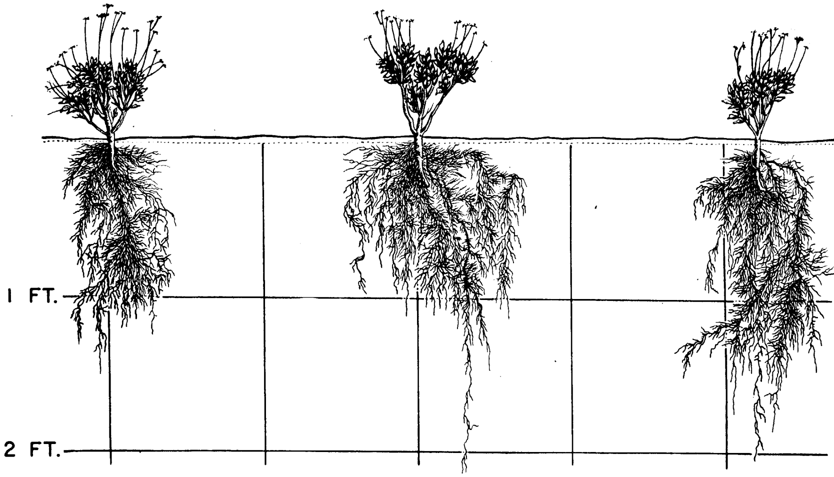

FIGURE 63.—Twenty-nine-month-old guayule transplants grown without irrigation in Bryant loam, mottled subsoil phase, in the Salinas Valley, Calif. A very dense claypan lay between 10 and 36 inches below the surface. Note the very poor root development despite the age of these plants.

plants were 29 months old. Note in figure 63 that a few roots had reached a depth of 24 inches and that all of the principal ones had reached depths of at least 12 inches. At least the upper 8 inches of the claypan had been effectively penetrated. However, considering the age of the plants involved, the degree of penetration was very poor. The plants were less than 8 inches tall; adjoining sites on Chualar loam (lacking claypan) bore plants of the same age measuring 16 inches tall and as much as 20 inches broad. No excavations were made here, but it may be presumed from the behavior of guayule in other similarly favorable sites that these larger plants had attained normal root depths, probably in excess of 15 feet.

HARD SURFACE LAYERS

Another form of impenetrable soil not involving waterlogging or poor aeration of the plant is found locally in the Salinas Valley. This consists of severe hardening within the surface foot, apparently resulting from compaction while wet and subsequent drying. The phenomenon has been noted in various degrees of intensity in loams, sandy loams, and gravelly loams of the Greenfield, Bryant, Hanford, and Chualar series. Because of the rapid formation of this hard layer, seedling roots are sometimes prevented by it from reaching the more favorable subsoil. Although the thickness and depth of the impenetrable layer vary considerably, its lower limit is almost invariably very close to 12 inches deep. It has been observed to range from 3 to 8 inches in thickness.

This hard layer is resistant to water penetration and difficult to wet by irrigation once it has dried out, but wetting is possible and has a very marked effect when accomplished. The resistant quality of the soil disappears entirely so that a bar may be pushed through it with ease. Subsequent drying produces a hard layer even harder than the first. Varying the depth of plowing apparently has no effect, and deep chiseling is ineffectual except in breaking up the continuity of the layer. After such chiseling large fragments of compacted soil have been observed exerting locally the same influence as the original hard layer.

Mechanical analyses of soil samples taken from above, within, and below a very hard layer revealed no significant differences in the sand, silt, and clay contents of the three samples. The percentage of clay within the hard layer was somewhat higher than that of the other two samples, and its moisture equivalent was about 17 percent as compared with 13 percent and 12 percent in the soil above and below the hard layer, respectively. These results do not appear to indicate sufficient reason for the localization of the hardening.

The hard surface layer has never been observed to affect the growth or root development of transplanted nursery stock, probably because the initially favorable conditions of the loam and the deeply planted taproot of the stock combine to permit deep root penetration within a short period. Seedlings, on the other hand, particularly if their root penetration is slowed either by low temperature or by seedling root rot on the young radicles, are likely to be trapped above or within the hardening layer. This manifests itself rather strangely. Several consecutive yards of one row may be occupied entirely by stunted plants exhibiting all the symptoms of having been pot-bound. The plants elsewhere in the same row or in an adjacent one may be quite normal and rapidly growing. Occasionally an otherwise normal row may contain one or a few short segments of stunted plants. In the early stages of seedling development such affected individuals may exhibit the appearance of drought-stressed plants and may even wilt or die although adjacent plants are growing lushly and moisture determinations reveal an abundance of water at and below a depth of 12 inches. This spotted distribution of trapped plants results partially from locally unfavorable conditions for rapid growth and partially from uneven development of the hard layer.

The effect on root development of being restrained above or within such a hard layer is very marked. From observation of many such plants in several stages and degrees of restriction and subsequent liberation, there may be hypothecated a history of very probable accuracy. The growing root, upon being restrained from further penetration, branches repeatedly. As each branch is stopped, it branches in turn until a mass of short, crooked roots are produced in the form of a coralloid mat, filling what space is available to the plant. Lateral roots, being higher in the soil and less promptly affected by hardening, take the lead and spread outward and downward until they too are restricted. If one of these should eventually find its way into a crevice with access to the subsoil, it will expand in the readily penetrable layers beneath the hard layer to form a reasonably normal root system. The stunted plant then recovers and continues its growth, but the coralloid mat in the crevices of the impenetrable hard layer remains as a relic from which the story of the plant's development may be partially deduced. Recovery from this form of stunting may be effected early in the plant's development by the softening of the hard layer by thorough wetting or by its fracture in plowing. In either case those plants whose roots find an outlet beneath the barrier show a marked recovery.

Figure 64 shows plants with their roots in all stages of restriction and evasion or release. The plants were growing in a deep phase of Bryant

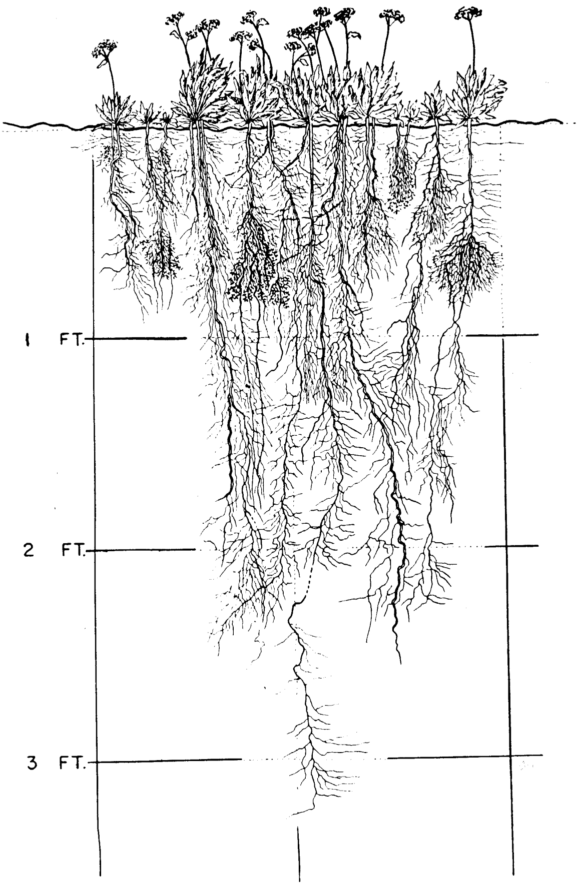

FIGURE 64.—Three-month-old guayule seedlings in Bryant loam, deep phase, in the Salinas Valley, Calif. A layer of hard soil had formed between 8 and 12 inches below the surface. Note the formation of coralloid mats of roots in and on the hard layer and the greater size of those seedlings whose roots have penetrated below 12 inches.

loam in which the hard layer was very irregularly developed. The lower limit of the hard layer was at about 12 inches below the surface. Although its average thickness was 4 to 6 inches, locally it approached within 2 or 3 inches of the surface of the soil. The plants were 3 months old when excavated on October 8, 1943. The very stunted individuals on both sides were still completely confined by the impenetrable layer, and their root systems included large coralloid mats. The two plants on the extreme right had finally found a route through the barrier, but their root systems still showed coralloid mats in the hard layer. Several of the larger plants near the center bore no coralloid mats and apparently had traversed the entire hard layer before hardening had advanced appreciably.

When this same planting was 4.5 months old, additional plants were excavated in areas in which there was a very severe hardening effect of the soil. The soil type at this site was Greenfield loam. Hardening had progressed to within 1 inch of the soil surface in some cases, and stunting of the plants was extreme. Figure 65 shows the entire root system of a very restricted plant. Its maximum penetration scarcely exceeded 4 inches and virtually the whole of its root system was composed of a coralloid mat. Figure 66 illustrates three such individuals; their vertical extension is shown in *A* and their lateral spread in *B*. The root systems of the two plants on the right show the mark of a chisel which passed through the soil within 5 inches of the plants at a time when the soil was too wet to break up the hard layer effectively. Their roots had grown into this chisel track and filled it with a coralloid mat. The soil had been so dry that the passage of a chisel opened a crack part way through the hard layer beneath the center plant. This plant is shown again in figure 67 as viewed in the direction of the row. The coralloid mat on the left occupied the chisel track previously described, while that on the right had formed in the crack across the row made by another chisel. This plant had reached a depth so near the lower limit of the hard layer of the soil that in another season with adequate moisture it would have freed itself into the permeable soil beneath.

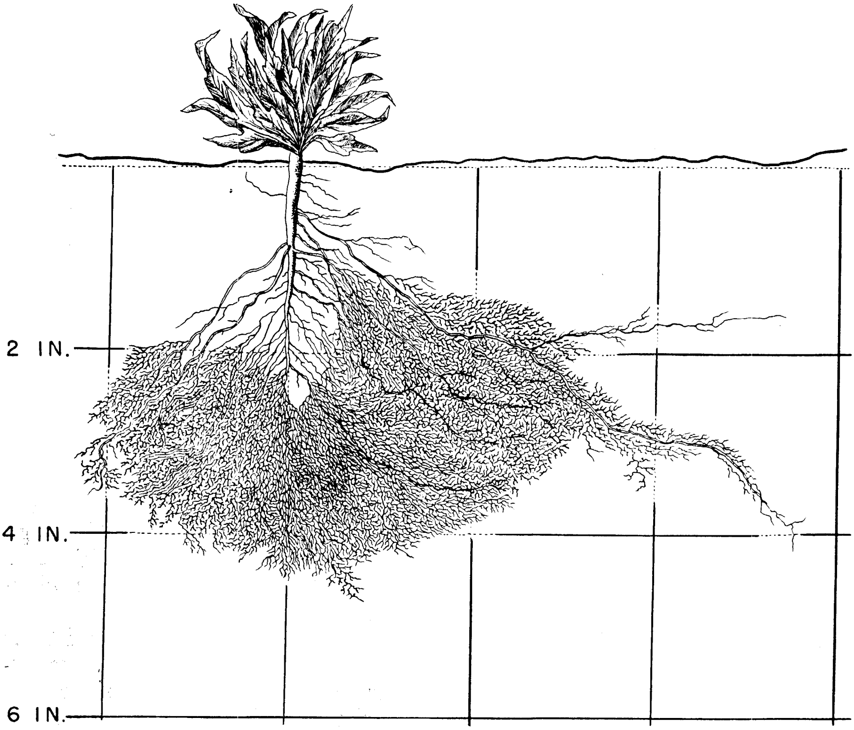

FIGURE 65.—A severely bound 4.5-month-old guayule plant from the planting shown in figure 64. The hard layer here was very hard and thick and close to the soil surface.

In early July 1944 still further studies were made of this same plot, then just a year old. Two excavations were made immediately adjacent to the sites just described and involving plants as nearly comparable with those of the earlier excavations as possible. Compare the 1-year-old plants in figure 68 with the 3-month-old ones in figure 64. At the end of a year's growth every plant had penetrated the hard layer and most

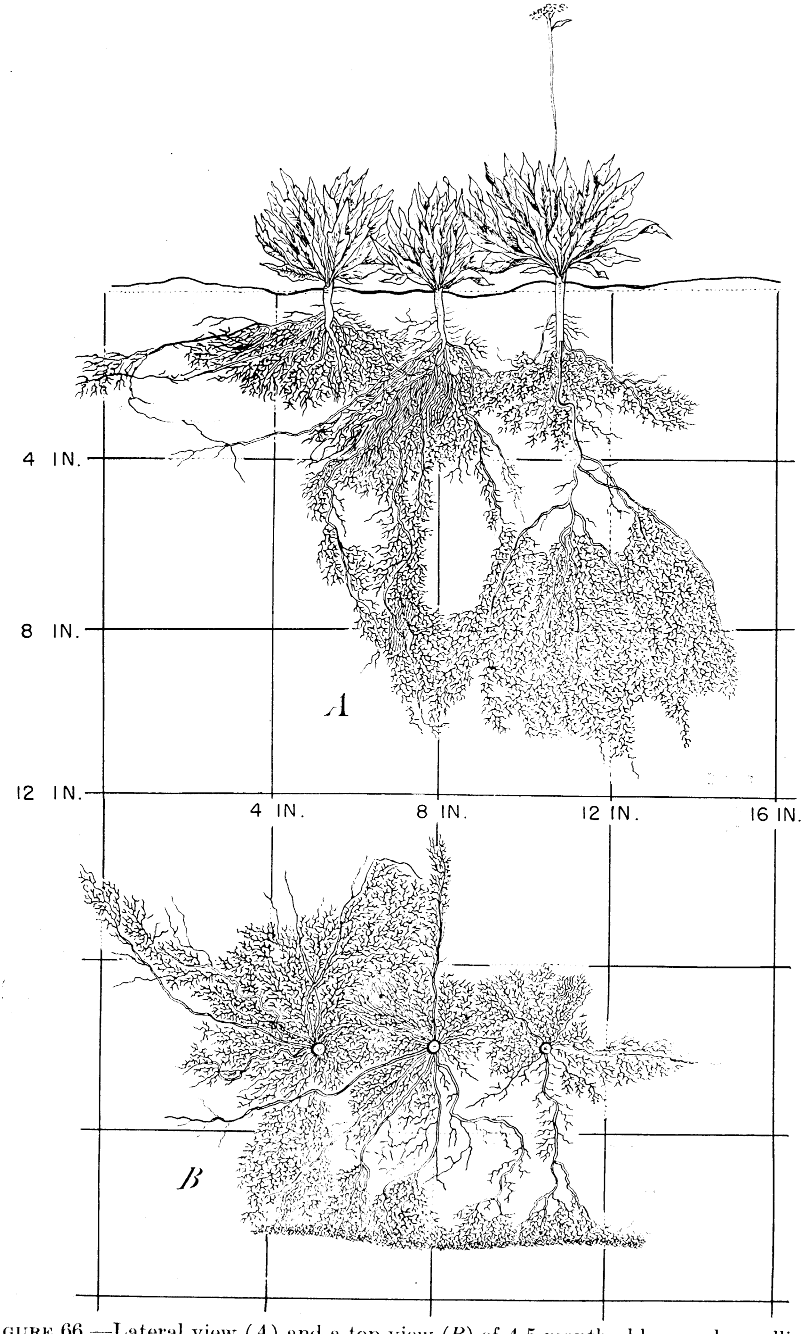

FIGURE 66.—Lateral view (*A*) and a top view (*B*) of 4.5-month-old guayule seedlings on a very hard layer adjacent to the site of the seedlings shown in figure 65. Almost the entire root systems consisted of coralloid root mats, and total penetration was less than a foot. Note the abrupt downward turning of the roots in an old chisel track at the bottom of *B*.

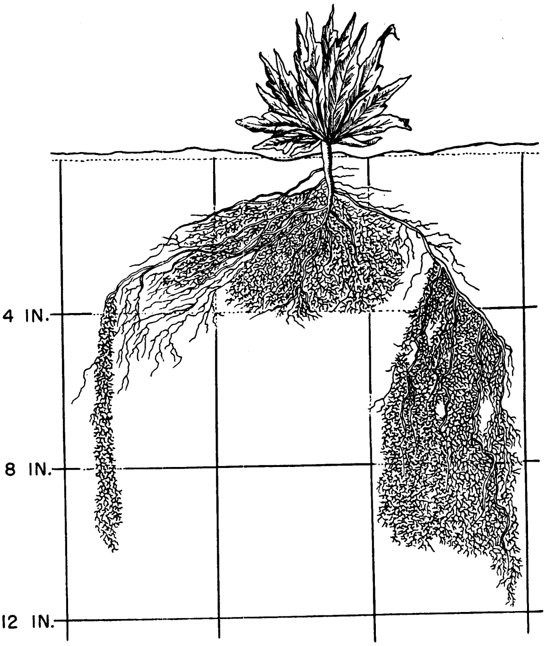

FIGURE 67.—The middle guayule plant shown in figure 66 viewed in the direction of the row. The coralloid mat on the left occupied an old chisel track parallel to the row; that on the right, a crack transverse to the row.

of them had reached a depth of 3 feet or more. The hardening of the soil at this site had not been so severe as elsewhere. Most of the stunted plants exhibited relic coralloid mats, but these had changed and lost their distinctive character and were not recorded in the drawing. The roots of the middle plants pictured in figure 68 show the results of persistent stunting probably brought about entirely by competition. The plants at the right and left in the illustration show the advantage of an early lead in growth.

The 1-year-old plants shown in figure 69 were excavated near the site from which those shown in figures 65 and 66 had been taken earlier. With the exception of some of the large plants near the center, all of them were at one time of the same class as those of the earlier excavation. The large individuals had encountered a break in the hard layer of the soil rather early, and the roots of several individuals had funneled down through this break. Their roots had spread laterally in the permeable soil beneath. Two plants just to the left of the center had more recently broken through the barrier. The remainder of the population remained completely restricted in the upper few inches of soil.

The mechanism by which root binding is effected in the hard soil layer is not fully clear. Apparently stoppage of root elongation and the formation of coralloid root mats often occur during the hardening of the soil, sometimes becoming quite pronounced before the resistance of the soil has reached what appears to be a serious degree. However, once compaction is completed and the layer is fully hardened, it is an effective mechanical barrier to further root penetration.

Guayule is not the only species affected by the hard soil layer. Figure 70 shows 4.5-month-old lettuce, guayule, and celery plants seeded simul-

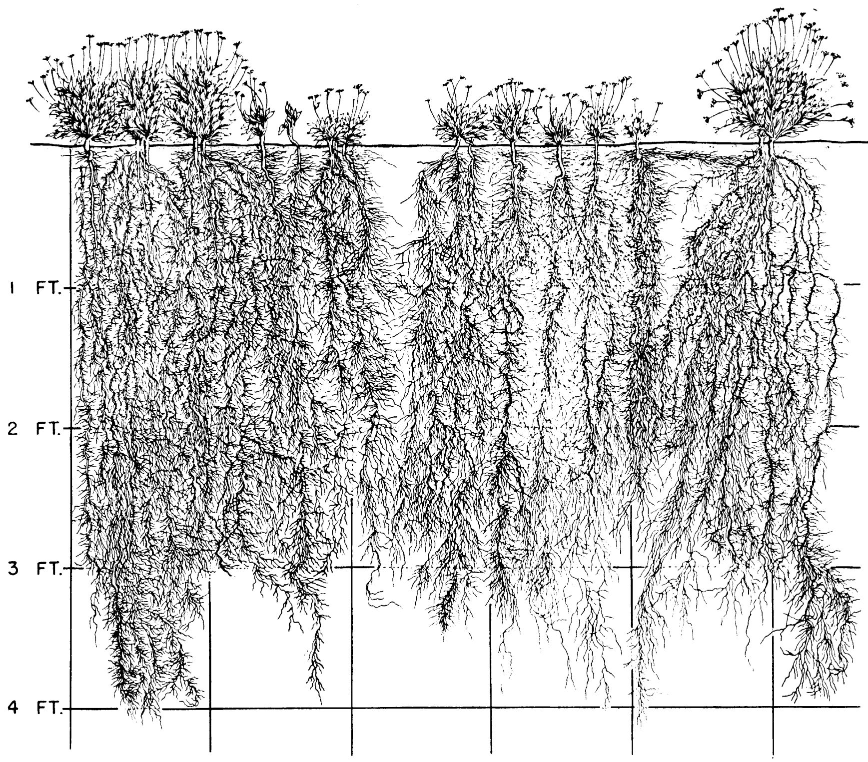

FIGURE 68.—One-year-old guayule plants adjacent to the site of the seedlings shown in figure 64. Although the winter rainy season had permitted all plants to pass the then softened hard layer of the soil, the great disparity of sizes resulted from the initial stunting by root binding.

taneously in Greenfield loam and excavated at the same time. The lettuce (*a*) consisted of three plants, each with one or two taproots and completely lacking in the mantle of fibrous laterals characteristic of the superficial levels in this species. The guayule (*b*) also consisted of three plants; the roots of one had been trapped in the hard soil layer. The roots of plants in the two rows of celery (*c* and *d*) were completely bound.

The effect of the hard layer in the surface soil is probably of more serious consequence in experimental plantings than in production plantings, but even in the latter it may assume important proportions. If as much as 10 percent of an area is affected, as was observed on two occasions, the reduction in yield would be economically very significant.

ROOT CHANNELS

Although the relation of root growth to old root channels, small animal burrows, and other openings has frequently been noted in other crop plants, it is probably of greater than ordinary importance in guayule. One is quickly impressed by the apparent weakness of growth in guayule roots, the profound effects of soil hardness on root habit, and the relatively trivial impediments required to stop growth. In most unfavorable soils, whether they be too hard for ready penetration, too light to retain

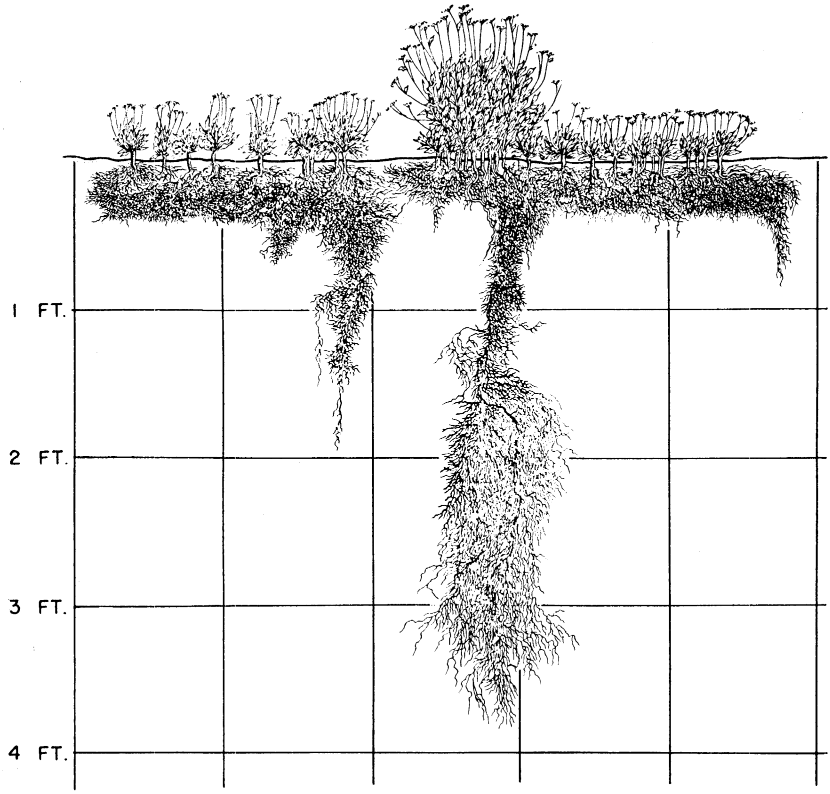

FIGURE 69.—One-year-old guayule plants adjacent to the site of those shown in figures 65 and 66. The highly developed hard layer of soil was softened only locally by the winter rains, and most of the plants remained root-bound. Note the normal root development below the 1-foot level and the larger tops of the plants thus freed.

moisture, or too dense or waterlogged to permit adequate aeration, the presence of root channels, animal burrows, or other continuous openings tends to mitigate the unfavorable condition. Such openings contain the organic debris deposited there by plants or animals as well as topsoil washed there by seeping water. In poorly aerated soils such material is more porous and therefore better aerated. In hardened horizons it affords a more readily penetrable route. In sands of very low water-holding capacity and low nutrient content it remains moist longer and contains more nutrients. It is not surprising, therefore, that guayule roots should develop luxuriantly in such channels.

Attention has already been called to the concentration of principal roots in old alfalfa root channels (figs. 53 and 56). In these instances the residual and washed-in debris of the channels were similar to the veins of clay in alleviating the effect of the very light sand in which they occurred. The same effect is seen in the concentration of feeder roots about the rotting roots of desert shrubs in Superstition sand at Yuma Mesa (fig. 49) and in depth of the guayule root following an old *Larrea* root channel (fig. 45).

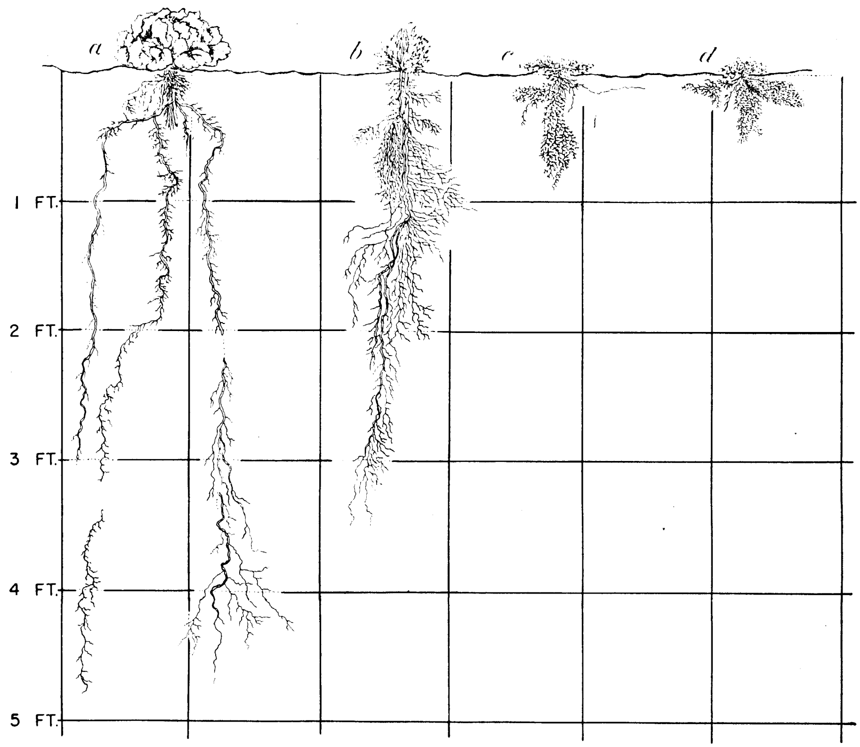

FIGURE 70.—*a*, Lettuce; *b*, guayule; and *c* and *d*, celery. All plants were 4.5 months old and had been grown in Greenfield loam in the Salinas Valley, Calif. A moderately hard layer had restricted the growth of superficial feeders in the lettuce, partially restricted the guayule (note the residual coralloid root mat), and completely bound the celery roots.

In resistant horizons, such as moderately developed claypans and caliche hardpans, roots of guayule were frequently observed to follow old root channels. Plants growing over claypan at Carrizo Springs (fig. 60) were able to penetrate the claypan only with difficulty except through old channels. Probably a third of the roots reaching the subsoil followed such paths. Often new roots were observed entering the still intact remains of their dead predecessors. The corky covering of the dead roots resisted rotting long after the wood had decayed. In a few instances, young roots occupied in this manner roots of the same individual that had been killed back the previous season by waterlogging in a claypan.

Although the abundance of nutrients in old channels and burrows is undoubtedly of value to the roots occupying them, the effect of moisture supply, aeration, and permeability on the growth and distribution of roots in such channels is strikingly clear.

SOIL TEXTURE IN RELATION TO ROOT-HAIR DEVELOPMENT

Soil texture influences in various ways factors required for the growth of root hairs in guayule plants, but position and frequency of irrigation may be equally influential. Root hairs are produced in guayule most copiously under conditions of low but adequate moisture and good aeration. In experimental greenhouse plantings it was frequently observed that reduction of water supply resulted in rapid and copious growth of root hairs. Similarly, whether the moisture supply was low or high, roots nearer the soil surface and therefore more subject to good aeration became more densely clothed in hairs than those deeper in the soil. It is not clear which factor is the dominant one, but that either may become limiting and prevent root-hair production is clear from field observations.

In the field it was noted that the more frequently dry and better aerated upper levels of the soil permitted much more copious growth of root hairs than did the lower levels. However, where the surface layers of soil are relatively heavy and the subsoil is porous (as in Anthony loam at Litchfield Park, Ariz.) the situation is reversed. The loam and the clay B horizon at Litchfield Park showed very scant root-hair development, but the porous caliche subsoil contained copiously hairy roots. No root hairs were ever observed in clay except where a root traversed a small opening in the soil. Even in such an opening if the root lay in actual contact with the clay, it produced no hairs on the side touching the clay but might be very hairy on the opposite side exposed to the soil atmosphere. However, if such a root grew into a large cavity in the soil, say an inch or more in diameter, those parts of the root surface remote from the soil would be bare of root hairs. If the root lay within 1 or 2 mm. of the soil, hairs grew out and established contact with the soil; but as soon as the root surface itself came into contact with the soil, no hairs were produced. It appeared that root hairs grew only when a space existed between the root and the clay and when that space was small enough to be bridged by root-hair production.

Apparently root hairs grow not only at the growing root tip but also on roots older than ordinarily observed heretofore. Young plants grown under irrigation and kept well supplied with water were found to be nearly devoid of root hairs. Subsequent observations of the same plot after the moisture supply had been depleted showed old and young roots of these plants to be well supplied with root hairs. The old roots involved still retained their epidermal cells in spite of some degree of apparent suberization, and the root hairs they bore were devoid of cytoplasm when observed. No extensive microscopic examinations were made of apparently hairless roots, but in a few instances roots were noted that bore only rudiments of hairs, low swellings on the epidermis. The relation of these primordia to the hairs of the copiously pubescent older roots is a matter for conjecture only, since all the older hairs observed were empty of cytoplasm.

Except on very young and actively growing roots no living hairs were observed, and it cannot be said at just what stage the once hairless roots produced their hirsute growth; but the evidence indicates that some such growth took place long after the differentiation and probably after the maturation of the root tissues. It was thought at first that none of the empty hairs were functional, but microscopic observation of such hairs on old roots brought in contact with a drop of water revealed this to be an error. The hair cavities were empty except for air. On contact with water, the porous but unbroken cellulose walls quickly absorbed water which began to accumulate in the lumina. The progress of this absorption could be watched readily by noting the quick diminution and occlusion of air bubbles. Unless the cortical tissues of the older roots bearing these empty hairs were suberized heavily, the absorptive activities of such a multitude of persistent root hairs must have been highly important to the water supply of the plant.

QUANTITY OF WATER SUPPLIED TO SOIL IN RELATION TO ROOT DEVELOPMENT

The availability of soil moisture to plants is controlled largely by soil type and texture. A number of phenomena observed in this study, however, indicate clearly that the availability of soil moisture to plants depends to some extent at least on the quantity of water applied to the soil rather than on the percentage of water the soil gives up to the plant.

DRYNESS OF SURFACE SOIL

The surface layer of soil nearly always dries out more rapidly than subsurface layers. In many cases, if rain and irrigation are infrequent or

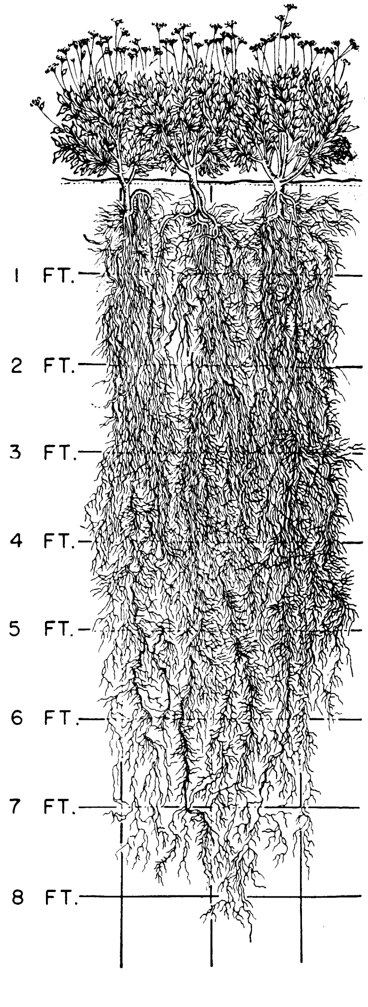

FIGURE 71.—Two-year-old guayule transplants grown without irrigation in Hanford sandy loam in the Salinas Valley, Calif.

are lacking during the warm season, the water content of the upper soil levels remains for long periods below the percentage required for root growth. Where moistening of the surface soil is very infrequent and light soil texture results in rapid moisture depletion, the effect on root physiognomy is limited even though root functions are locally stopped. Throughout this study it was noted that there was only a slight reduction of root density in the upper 6 inches of soil with a relatively dry surface as compared with soils having considerable surface moisture. The plants pictured in figure 71 were grown without irrigation in a light phase of Hanford coarse sandy loam in the Salinas Valley and were 2 years old when excavated in mid-July 1944. Compare the root distribution in the upper foot of soil in plants shown in figure 71 with that in plants taken from any of the more constantly moist soils; for example, those in a lighter and sandier but frequently irrigated soil (figs. 59 and 60) and in a moist but unirrigated clay (fig. 58).

More significant than the reduction of root density in dry soil is the very high percentage of roots surviving long periods of severe drought in surface soils. With the coming of drought the youngest and tenderest roots may fail to survive, but the older ones quickly suberize and remain dormant but alive for months in apparent readiness for further moistening of the soil. Rarely does one encounter a root dead of drought even in surface soils that have been wholly depleted of chresard for a period of as much as 5 months.

In greenhouse experiments in which half the roots of each of a number of guayule plants were left to dry and deprived of further irrigation for over 6 months, the dry roots showed little necrosis while being dried and none thereafter.

The drying of surface-soil layers is general in the Southwest, and the survival of dried roots is also general among native and crop plants. Only in perennial plants is it of great importance, for only they are required to recover and resume growth after long periods of drought dormancy. The presence of a dense growth of dormant roots in the surface soil enables the plant to utilize quickly light rainfall or irrigation.

DRYNESS OF SUBSOIL

In permeable soils water penetration is so rapid and extensive that dry horizons in the subsoil, if they occur at all, are beyond the penetration of guayule roots. This is not the case, however, in areas of very light rainfall or of impermeable soils. In the Rio Grande Valley of Texas, from Del Rio to McAllen, there is a band of alluvial soil of very poor permeability to water. At Rio Grande City a boring in Laredo silt loam after a 3-inch rainfall revealed a total moisture penetration of less than 36 inches. This soil is exceedingly deep and homogeneous. Runoff here is impressive, but no data are available on the percentage of rainfall thus lost. Normally no heavier rainfall or equivalent heavier irrigation occurs in this area, and water penetration usually cannot be expected to exceed 36 inches.

A study of 2-year-old guayule at Rio Grande City about the middle of March 1944 included both plants grown under irrigation more or less constantly since planting and those established under irrigation for 3 months and thereafter dry-farmed. The average annual rainfall of this area is about 17 inches, but the total recorded during the first season's growth of the guayule was only about 12.5 inches.

Although the growth rate of the guayule in Laredo silt loam was very high, root development does not reflect top size. Figure 72 shows the root systems of plants grown under irrigation for 2 years. Note that top growth was heavy but the root systems were neither extensive nor dense. In the process of making the excavation particular attention was paid to soil moisture, but no sign of moisture was encountered above a depth of 10 feet where the upper fringe of some form of water table was touched. The roots, however, reached a depth of only 5 feet, and their sparseness at that depth suggested low moisture content at the time of their growth there. The poor soil occupation by the roots and the excellent top growth would indicate that an abundance of moisture was supplied by a relatively small volume of soil and that the shallowness of moisture did not serve to limit top growth during the growing season. At the time of the excavation, of course, no moisture had been added to the soil for several months, and the powder-dryness of the soil was reflected in the very dormant condition of the plants.

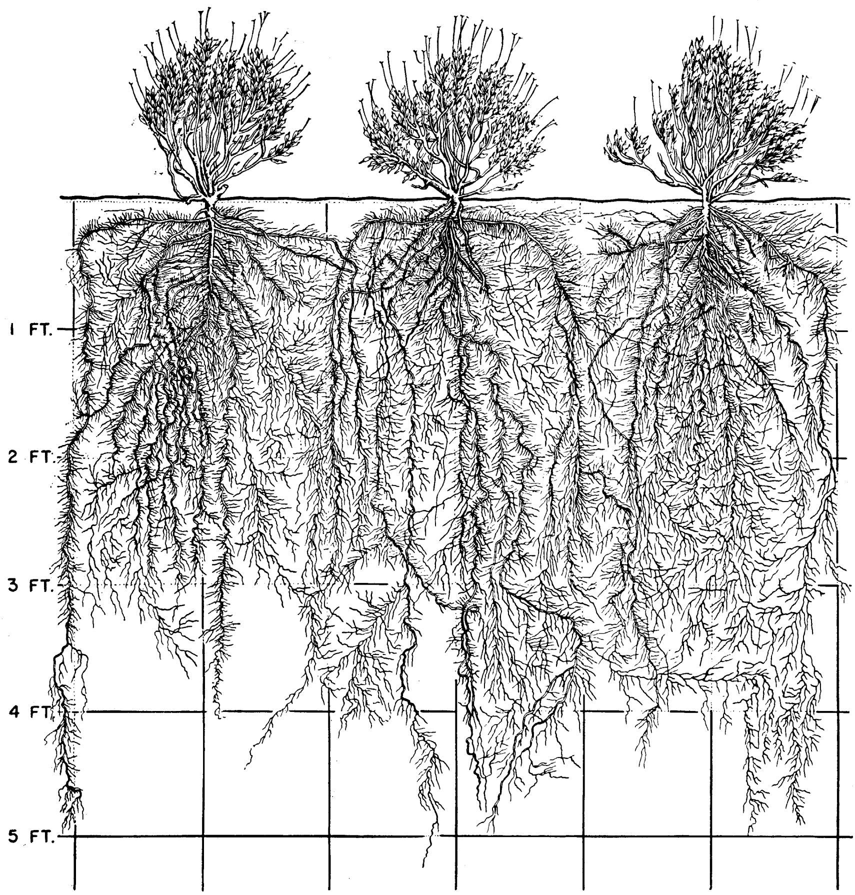

FIGURE 72.—Two-year-old guayule transplants grown under irrigation in Laredo silt loam at Rio Grande City, Tex. Note the very good root development in the upper few feet and the very shallow total penetration caused by dry subsoil.

The unirrigated plants shown in figure 73 were not nearly so large as the irrigated ones in figure 72 and their root penetration was less than 4 feet. The penetration of moisture was even less in this case than in the irrigated plot. Here, too, the soil was found to be very dry throughout the 6-foot depth examined

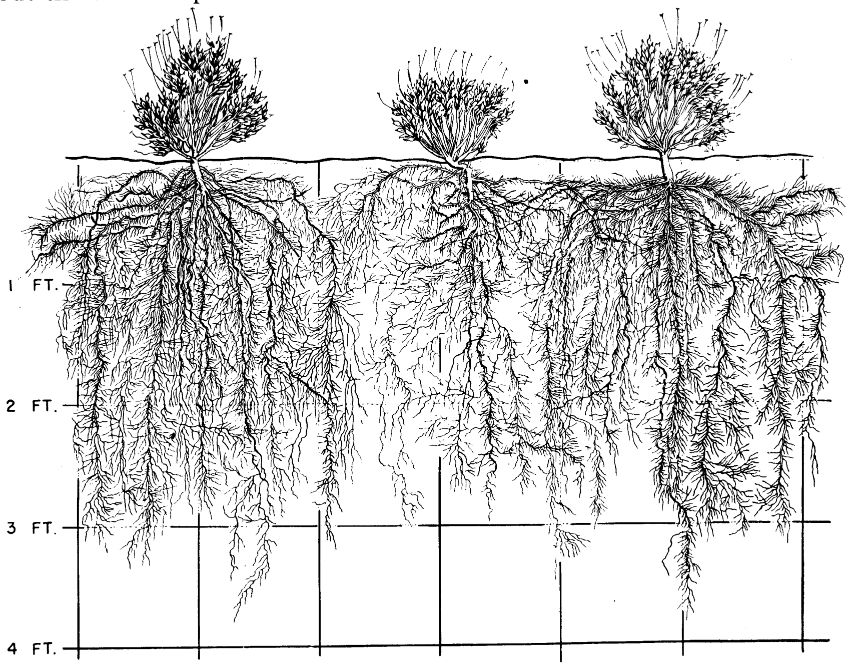

FIGURE 73.—Two-year-old guayule plants grown without irrigation and adjacent to those shown in figure 72.

Shantz (*14*) stated that drought-resistant plants (those that store water and reduce transpiration sufficiently to remain physiologically active in spite of drought) are able to push their roots into dry soil. This ability, he stated, is not shared by ordinary field crops. Hendrickson and Veihmeyer (*8*) showed that bean and sunflower (neither drought-resistant nor drought-enduring plants) were unable to penetrate dry soil by means of root growth. The evidence of guayule in Laredo silt loam would indicate that drought-enduring species also are unable to penetrate dry but friable soil.

If the root development of the Rio Grande City plants (figs. 72 and 73) is compared with that of plants grown over moist subsoil (figs. 17, 39, 40, 58, 71, 74, and 96 (p. 110), for example), two facts are immediately evident: (1) The depth of penetration was not nearly so great at Rio Grande City; and (2) the total absorbing surface of the Rio Grande City plants was proportionately much less than that of those elsewhere. Yet, a comparison of the top sizes reveals that the irrigated plants at Rio Grande City were as large as any of the others and much larger than some. A comparison of the moisture equivalents of the several soils indicates no possible reason why top growth at Rio Grande City should have been so successful in spite of limited extent of the root systems. In the very homogeneous Rio Grande City profile a sample from a depth of 30

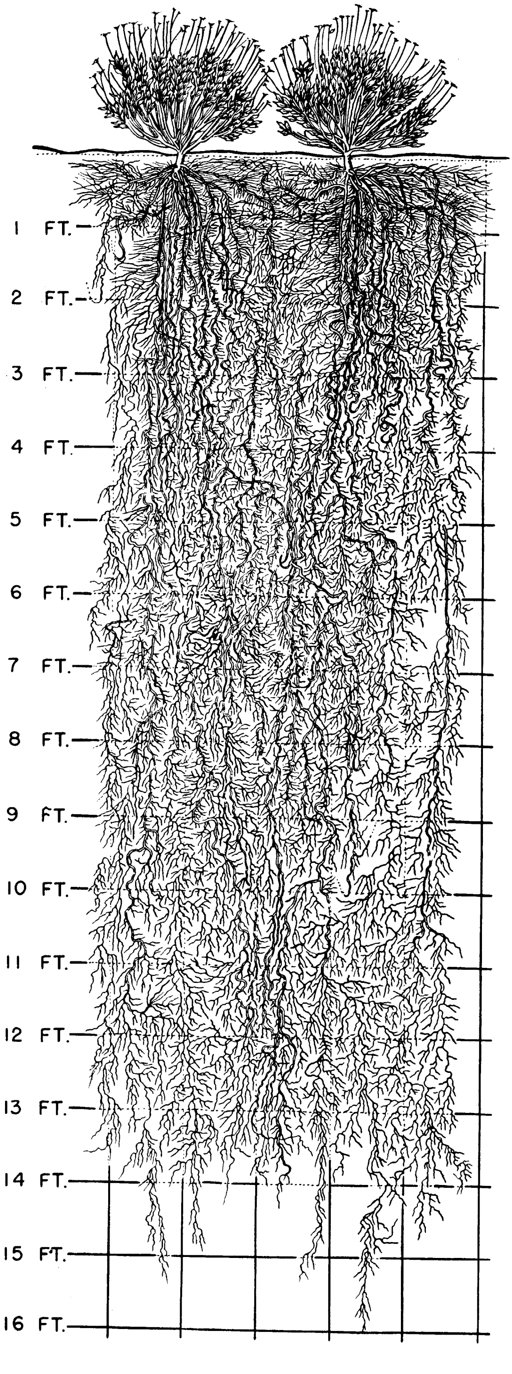

FIGURE 74.—Two-year-old guayule plants spaced at 24 inches within the row and grown under irrigation in Anthony loam at Litchfield Park, Ariz.

inches had a moisture equivalent of 21 percent and that of several horizons at San Antonio ranged from 23 to 27 percent, that at Litchfield Park from 7 to 18 percent, and that of the Salinas Valley from 5 to 12 percent. The size and density of the root system seem to be in no manner related to the water-retentive power of the soil so long as that factor is not extreme or accompanied by some detrimental soil character such as claypan.

Jean and Weaver (*9, p. 63*), working with field crops under varying drought stress, reported "a striking correlation between the growth of underground and aerial plant parts." It appears that a correlation exists between aerial growth of guayule plants and frequency of irrigation or rainfall (or constancy of available water), while another correlation obtains between extension of root system and volume of favorable soil available. The correlation between top and root sizes breaks down in this case. Further observations pertinent to these relations are given in the next section.

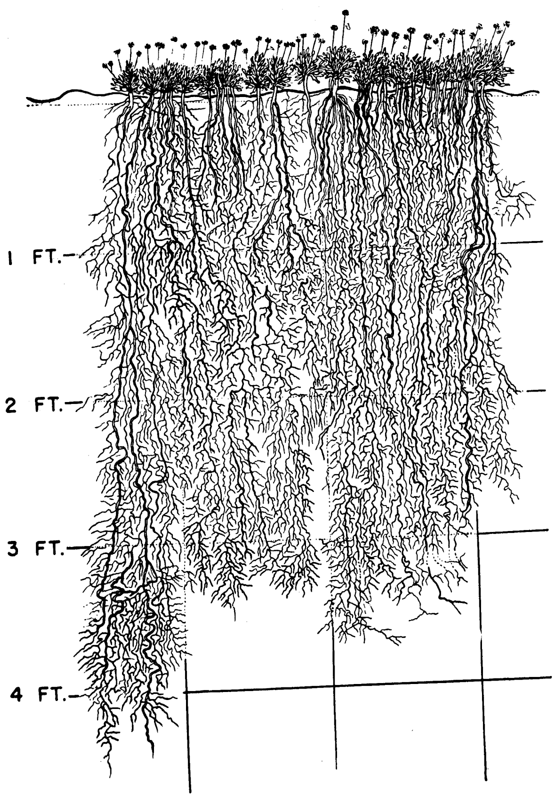

FIGURE 75. —Four-month-old nursery plants of guayule (dry) in Chualar loam in the Salinas Valley, Calif.

FREQUENCY OF IRRIGATION

As was indicated in experiments on the irrigated and dry-farmed plots at Rio Grande City, root habit is not influenced to any great extent by frequency of moisture availability but this factor does influence considerably the size of plant tops. Conrad and Veihmeyer (*6, p. 132*) concluded that—

if the soil is wet at the beginning of the growing season to the full depth to which roots of plants would normally penetrate, subsequent additions of water by rain or irrigation, unless adverse conditions for growth are brought about thereby, can have but little influence on the extent of the root system developed.

In some irrigation experiments [8] involving nursery plantings in Chualar loam in the Salinas Valley, a series of excavations were made in nursery beds grown under various moisture conditions. The plantings had been subjected to the several treatments after a 7-week establishment period with standard nursery irrigation. One treatment was left unirrigated from July 24 until after the date of the excavation, about October 1, 1943. The remaining treatments consisted of irrigating each plot when the soil reached a given moisture stress. Since the lower stresses were reached sooner than the higher ones, some plots were irrigated as often as twice or three times a week during seasons of higher temperatures whereas others received water less than half as often. For purposes of discussion the treatments will be referred to as dry, moderately irrigated, and frequently irrigated. The 4-month-old plants of these several plots are illustrated in figures 75, 76, and 77, respectively.

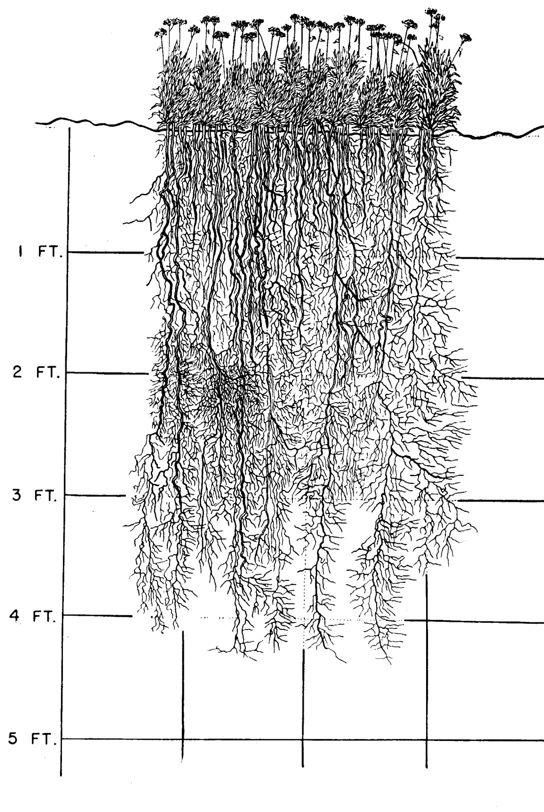

FIGURE 76.—Four-month-old nursery plants of guayule (moderately irrigated) in Chualar loam in the Salinas Valley, Calif.

[8] Designed by Kelley, Hunter, and Hobbs (*10*).

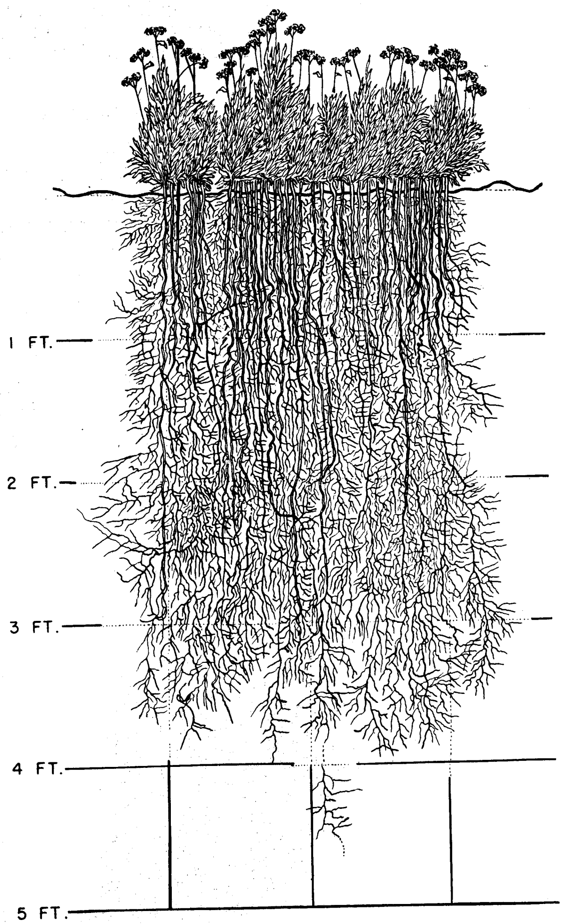

FIGURE 77.—Four-month-old nursery plants of guayule (frequently irrigated) in Chualar loam in the Salinas Valley, Calif.

The root habits of the plants given the various treatments do not differ in any significant degree. The irregular depth of penetration of the roots of the plants illustrated in figure 75 was not the result of the dry treatment (for in all three plots the subsoil was moist) but was caused by an irregularity in the claypan of the Chualar loam in which the plants were grown. Another excavation in a plot given the dry treatment showed uniform penetration to 4 feet. Some degree of irregularity was induced by the severity of competition for moisture. The weaker seedlings were eventually killed out completely in the dry treatment, whereas they persisted much longer in the moderately or frequently irrigated treatments. Root density was comparable in the three treatments. Apparently in all three cases the soil had accommodated what roots it could, and the differences between the treatments lay in the quantities of water available for absorption in the several comparable volumes of soil. This is reflected in the size of the top growth and not in the root habit, as indicated by the very lush top growth of plants given the two irrigated treatments and by the stunted seedlings in the dry treatment.

FLUCTUATION OF WATER TABLE

Observations on guayule growing above shallow water tables have been very scanty. Only one excavation was made involving a temporary water table at a depth of about 15 feet in the clay and caliche subsoil of Lewisville silty clay at San Antonio. By pumping from a sump in one end of the pit, it was possible to keep the water level down to 16 feet for a period of study but the ends of the roots could not be reached.

A very heavy rain fell on the unirrigated guayule planting at San Antonio shortly before excavation was begun for a root study. As much as 4 weeks after the rain, when the root study had been completed, the water table stood at 15 feet in spite of repeated pumping meanwhile. The soil in the bottom of the pit was observed with the aid of an auger to a depth of 20 feet where a dry, impervious clay was encountered. The presence of this layer and the recent heavy precipitation were the bases for concluding that the water table was temporary. However, at the end of 27 days of immersion the roots observed below the 15-foot level showed no sign of ill effect. As indicated in figure 58, the roots showed little evidence of having reached their extremities at 16 feet. It is possible that some of the principal roots terminated in the impervious clay layer at 20 feet.

Further evidence of the temporary nature of the water table at San Antonio is the fact that the guayule plants there were repeatedly observed in a state of drought dormancy during periods of deficient rainfall. This is quite contrary to the condition reported from the Mesilla Valley of New Mexico.[9] The permanent water table there varies between 6 and 7 feet in depth. This water table is the result of seepage from a large irrigation canal. Two plots about 18 months old—one irrigated and one unirrigated since establishment—showed remarkably little difference in growth, although the average annual rainfall of that area is only about 8.5 inches and cultivation without irrigation is considered impossible. The constant verdure of the unirrigated planting was conclusive proof that plants were receiving moisture from the water table. However, since no excavation was made there, it is not possible to state whether the roots invaded the waterlogged zone or merely fed on the capillary fringe; nor is it possible to judge whether any injury resulted from the 1-foot fluctuation in water level. Inasmuch as both rubber production and frost resistance are thought to depend in some measure upon effective dormancy, such a situation is probably unfavorable to guayule culture, especially in areas subject to low temperatures.

WATERLOGGING

It is difficult to distinguish between plants that have actually been drowned and those in which root and crown diseases have been induced by periods of inundation, too wet soil, and other factors. It has been observed that young guayule plants could stand several hours of complete immersion without ill effect on some soils, such as Rio Grande undifferentiated alluvium at Presidio, Tex. A short time after this inundation took place, however, a flood of 3 days' duration killed the entire planting. At Carrizo Springs on Crystal fine sandy loam and at Rio Grande City on Laredo silt loam (the latter very similar to the Presidio alluvium) short

[9] Correspondence to the author from C. H. Davis, Special Guayule Research Project.

periods of inundation of the crowns alone resulted in heavy losses; and even heavy irrigation alone, without any flooding of the crowns, caused losses. Whether these were primarily cases of drowning or of infectious disease is difficult to say.

In many instances soils with poor subsurface drainage caused by claypans have been found to contain plants with a few or several of their roots dead and rotting. This was observed particularly in Crystal fine sandy loam, fine-textured subsoil phase, at Carrizo Springs (fig. 60) and in Greenfield coarse sandy loam overlying old Bryant claypan horizons in the Salinas Valley (fig. 57). At Carrizo Springs the waterlogging occurred at about 18 inches, while in the Salinas Valley the depth was 3 to 8 feet. In these instances the rotting did not progress to the whole root system. The damage apparently occurred repeatedly, new losses resulting from each instance of waterlogging and new roots being produced during each interim.

Severely developed claypans in Bryant loam in the Salinas Valley often show such striking mottling as to indicate long periods of waterlogging. As pointed out earlier, the plants illustrated in figure 63 had sent their roots through such a waterlogged horizon and into the nearly impermeable claypan. Excavated at an age of 29 months, they showed no sign of root loss and suffered only from stunting caused by restriction of their root systems. Where these claypan spots cause depressed hogwallows, a great many guayule plants are lost, apparently from drowning of the lower parts of their root systems. After too heavy irrigation they show no ill effect until the surface soil layer dries out and the shallow remaining roots are no longer moist. With continued lack of moisture such plants finally die of drought.

At one site in the Salinas Valley, an overflowing tail ditch flooded and killed a great many young guayule plants on Bryant clay loam. Only those plants whose crowns were actually touched by water were killed. If a plant occupied a small hummock that projected above the surface of the water even as little as a quarter of an inch and consisted of an area as large as 3 or 4 square inches, the plant was unharmed. An inspection of the soil immediately behind the receding water revealed that the soil was saturated only in the surface few inches and that slow penetration of the compacted upper layers had prevented waterlogging of the deeper soil layers. Fragments of roots dug from the deeper soil layers were still alive although their parent plants had been rotted through above them.

Excessive water seems to do little or no harm at very deep levels in the soil, as observed in the case of the temporary water table at San Antonio. At depths of a few feet root loss is moderate, while at only 18 inches, as at Carrizo Springs, the loss is severe and considerable stunting of the plant results. Surface inundation is often fatal to the plant. For this reason, depth of permeable soil is one of the most important factors in successful guayule culture. The survival of the plants shown in figure 63, in spite of shallow waterlogging, remains the unexplained exception.

Effects of Competition of Various Kinds

It has been pointed out that guayule is a very poor competitor. Competition affects it adversely not only by reducing its rate of growth but also by effectively preventing its survival outside of cultivation in all but a very limited natural range. In this respect it is not unlike most of our crop plants. The situation differs, however, in that guayule is being cultivated nearer its native habitat and under climatic conditions more similar to its natural range than almost any of the other cultivated species of the Temperate Zone. Even on the tilled soils within its natural range guayule is unable to stand any great amount of competition.

The literature covering the general field of plant competition has been reviewed in detail by Clements, Weaver, and Hanson (*5*). The plant-competition concept has received a great deal of attention from physiologists, ecologists, and agronomists as applied to a wide variety of species both in natural vegetation and in cultivation, as well as in the greenhouse and laboratory.

COMPETITION OF GUAYULE WITH WEEDS

Perhaps no more striking illustration of the role of competition in guayule growth can be found than the effects of various degrees of weed competition. Opportunity for an investigation of this was afforded as a byproduct of an experiment [10] in weed control in nursery beds. Three beds were sown April 28, 1944, on Greenfield sandy loam in the Salinas Valley. They were irrigated according to standard nursery practice, but there was a tendency toward drought not ordinarily permitted. This served to intensify competition for soil moisture. Bed A was hand-weeded four times in May and June. Figure 78, *A*, shows that the population of this bed as of August 3, 1944, consisted of 229 guayule plants per square yard and no weeds. Bed B was sprayed on May 2, 1944, with 100 cc. of 5-percent tar oil per 20 square feet and received no further treatment. Figure 78, *B*, shows that the population of this bed in August consisted of 113 guayule plants and 55 weeds of various species per square yard. Bed C was sprayed on May 1, 1944, with 60 cc. of stove oil per

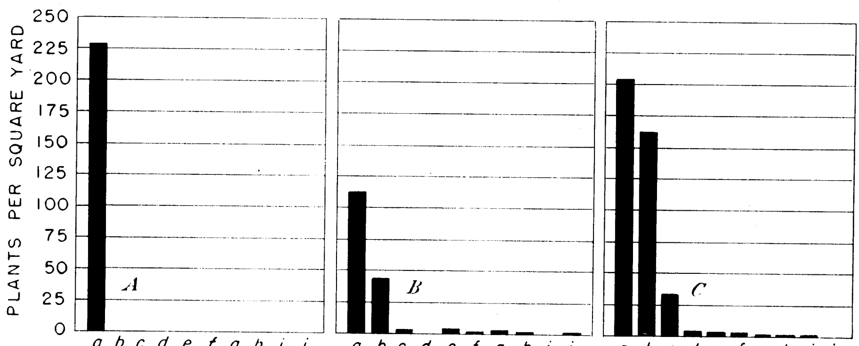

FIGURE 78.—Plant populations in nursery beds subjected to various weed treatments: *A*, Guayule free of weeds (see fig. 79); *B*, guayule with moderate weed competition (see fig. 80); *C*, guayule with heavy weed competition (see fig. 81). *a*, *Parthenium argentatum;* *b*, *Anagallis arvensis* L.; *c*, *Polygonum aviculare* L.; *d*, *Platystemon californicus* Benth.; *e*, *Convolvulus arvensis* L.; *f*, *Capsella bursa-pastoris* (L.) Medic.; *g*, *Silene gallica* L.; *h*, *Medicago hispida* Gaertn.; *i*, *Erodium cicutarium* (L.) L'Her.; *j*, *Poa annua* L.

[10] Designed by H. M. Benedict, Special Guayule Research Project.

20 square feet and received no further treatment. The population of this bed in August, shown in figure 78, *C*, consisted of 203 guayule plants and 207 weeds of various species per square yard.

The three beds were excavated in early August when the guayule was 14 weeks old. The root development of the weed populations was not studied in detail, but observations in the course of the study revealed that the weed roots corresponded in density approximately to the num-

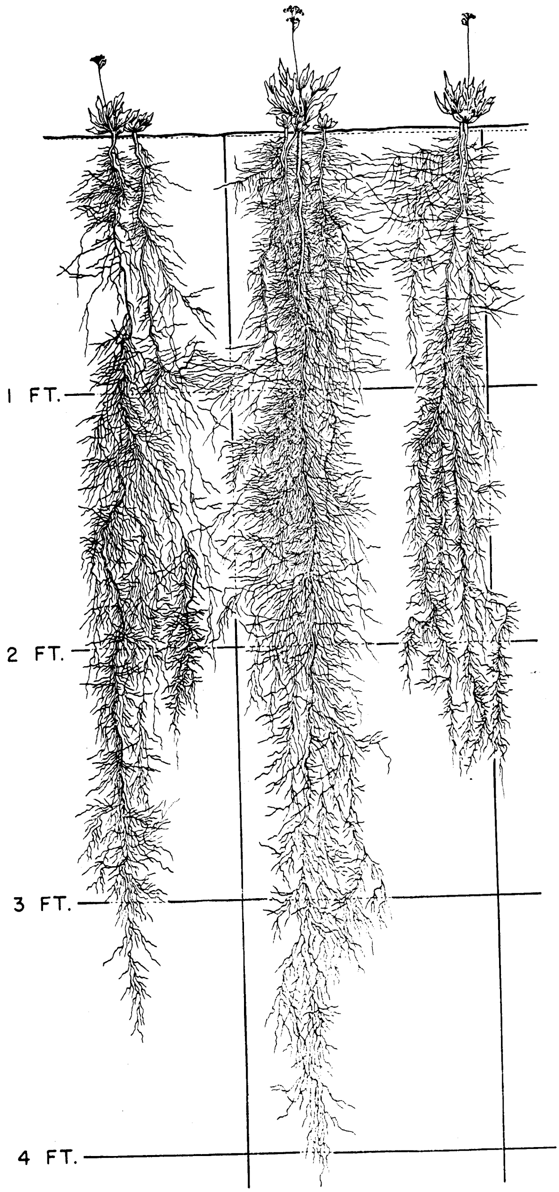

FIGURE 79.—Fourteen-week-old nursery plants of guayule grown free of weed competition in Greenfield sandy loam in the Salinas Valley, Calif.

ber of plants present and the density of ground cover they afforded. Their feeder roots were concentrated in the first foot of soil, and below a depth of 18 inches they offered little competition to guayule. Representative guayule plants were studied in each bed in a trench dug across the rows. Figure 79 shows plants from bed *A*, which developed free of weed competition. In both top and root development they corresponded to the growth of plants under drought stress shown in figure 75 at an age of 4 months. They occupied the soil rather fully, and their feeder distribution was fairly even. The plants in bed *B* (fig. 80) showed the effect of weed competition rather markedly. The top growth and total root penetration were much reduced and the production of feeders in the

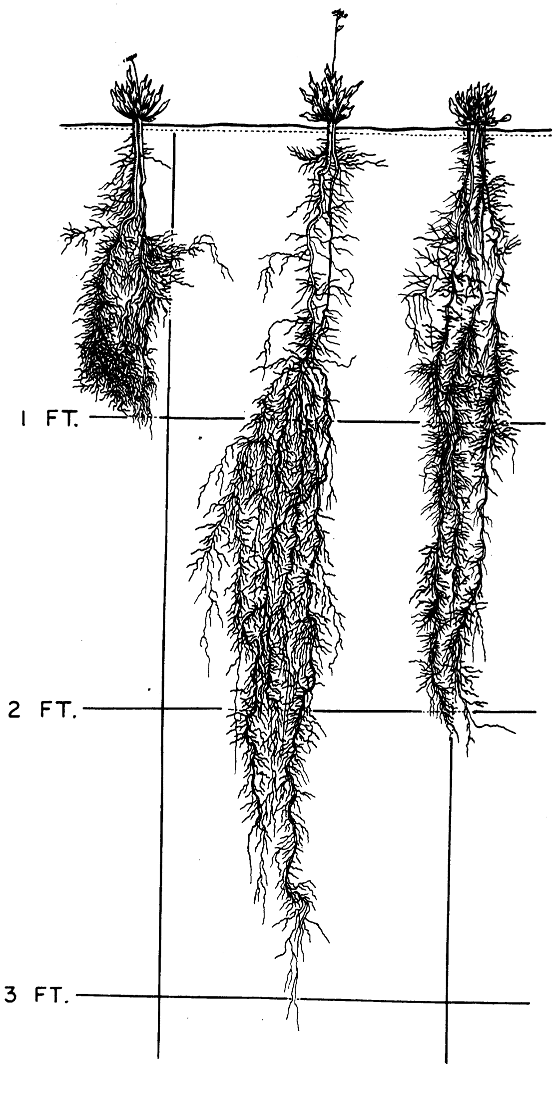

FIGURE 80.—Fourteen-week-old nursery plants of guayule grown with moderate weed competition adjacent to plants in figure 79.

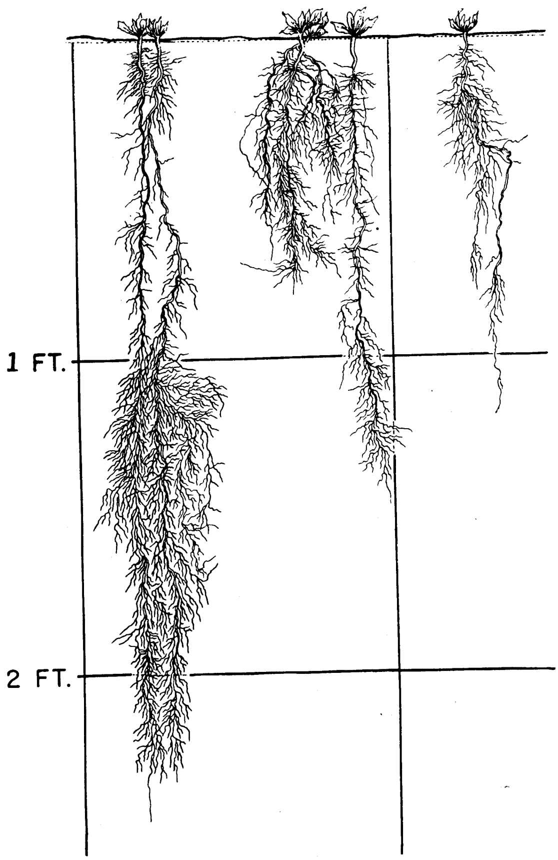

FIGURE 81.—Fourteen-week-old nursery plants of guayule grown with heavy weed competition adjacent to plants in figure 80.

upper foot of soil was very poor. Weed competition undoubtedly depleted the moisture content of the upper soil layers before the guayule could gain control there. The top growth and root penetration of the plants in bed *C* (fig. 81) were still further reduced by very heavy weed competition, and their feeder distribution was irregular almost throughout.

One fact is strikingly clear from a study of the three groups of plants. The natural tendency of the surface soil to be early depleted of moisture is much augmented by the presence of weeds. The much more normal branching of guayule roots at the depth of 1 foot and below indicates that the competition offered by the weed species here involved is very effective in the upper soil levels. Not only survival but some degree of recovery of the guayule plant that reaches well into the second foot of soil in spite of heavy weed competition may be possible.

It is significant that, with the exception of *Convolvulus arvensis*, which was not one of the more important species, all the weed species encountered in this experiment were annuals. They were therefore at the seedling stage simultaneously with the guayule. Many plants of *Anagallis arvensis* exhibited stunting quite as striking as that of guayule, but in general weed growth was luxuriant.

COMPETITION BETWEEN GUAYULE SEEDLINGS OF EQUAL AGE

Competition between guayule seedlings of equal age differs considerably from competition with weeds. Most ruderal species are more vigorous in the seedling stage than is guayule, and they are capable of winning an advantage which results in a partial suppression of guayule growth. To the extent that guayule germinates irregularly in pure stands some individuals gain a similar advantage of priority over others. Such stands are usually unnecessarily dense, however, and the suppressed individuals constitute no loss. In a nursery experiment [11] on Chualar loam in the Salinas Valley, seedling stands of guayule were thinned to various den-

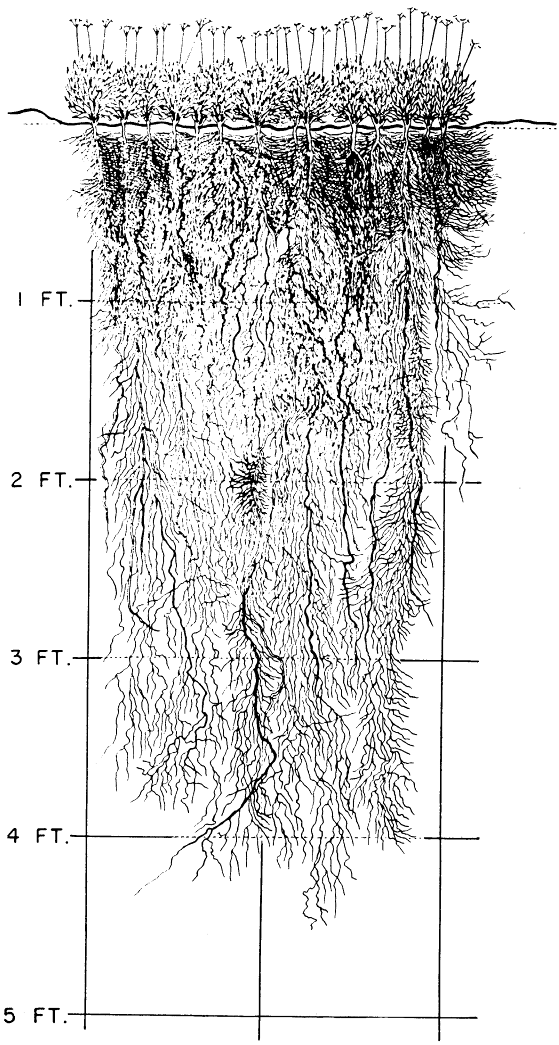

FIGURE 82.—Five-month-old nursery plants of guayule from a stand thinned to 10 plants per square foot grown in Chualar loam in the Salinas Valley, Calif.

[11] Designed by W. A. Campbell, Special Guayule Research Project.

sities in order to study the effect of competition on top growth and disease. The process of thinning eliminated the tardy seedlings so that a high degree of even-agedness resulted and suppression of some individuals to the advantage of others was reduced to a minimum.

The plots were sown May 26, 1943, kept free of weeds by hand weeding, and irrigated moderately until July 22 and heavily thereafter. Excavations were made between October 16 and 21, 1943, when the plants were about 5 months old. Three selections were made from the several den-

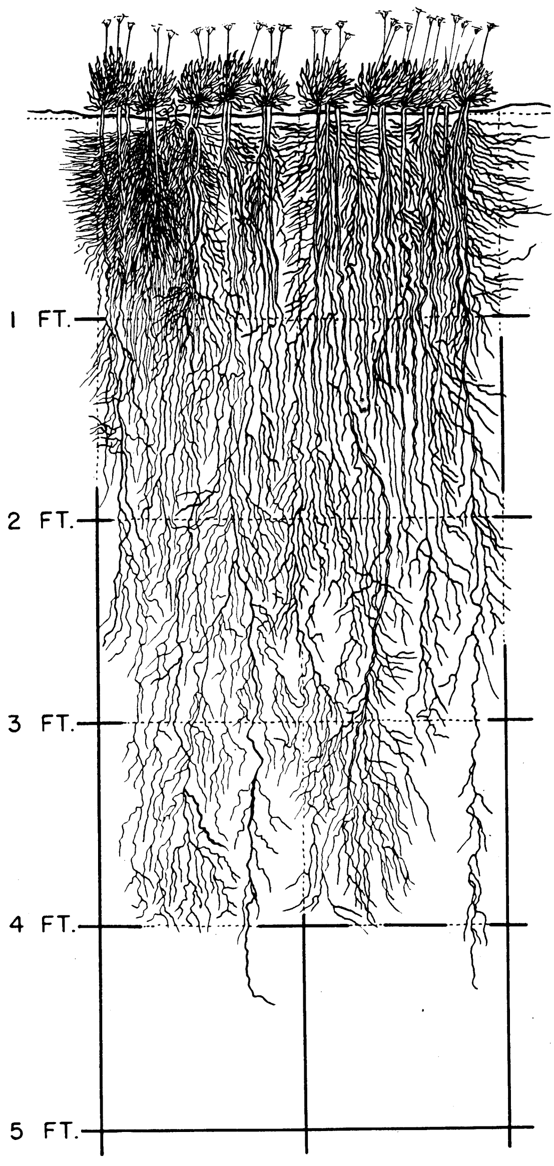

FIGURE 83.—Five-month-old nursery plants of guayule from a stand thinned to 30 plants per square foot near those shown in figure 82.

sities, involving plots with 10, 30, and 50 plants per square foot (figs. 82–84).

In the process of making the excavations it was discovered that the claypan, which characterizes this soil, occurred at various depths in this locality. In every case the guayule roots penetrated the claypan from 1 to 1.5 feet. This resulted in a considerable differentiation in depth of penetration, which accidentally was deepest in the thinnest stand and shallowest in the densest stand. Differences in root depth shown in the results to be correlated with density of stand cannot be ascribed to competition.

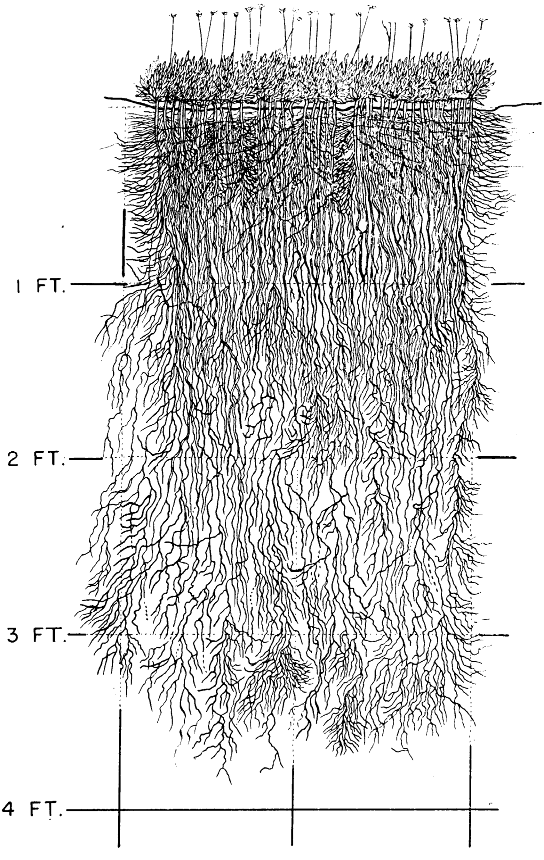

FIGURE 84.—Five-month-old nursery plants of guayule from a stand thinned to 50 plants per square foot near those shown in figure 82.

No very great difference in density of soil occupation occurred in the roots of the plants of the three classes, the outstanding difference being the somewhat greater density of the roots in the upper foot of soil in the thinnest stand (fig. 82). As in the case of differential irrigation, varying density of stand seems to have effected no change in density of root dispersal, this factor apparently being relatively constant for a given volume of any soil type. Reduction in space per plant had decreased, therefore, the number and spread of roots per plant, the individual root systems of the more widely spaced plants being by far the strongest.

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This is clearly reflected in the size of the aerial parts of the plants produced. The denser stand always produced the smaller tops. In this experiment the heavy schedule of irrigation after July 22 had the unfortunate effect of reducing the severity of competition and therefore partially masking the effect.

EFFECT OF COMPETITION ON ROOT HABIT

That the vertical habit of growth of guayule root systems is the result of competition is clearly evident from the greater spread of roots on the open sides of guard rows, at the ends of rows, and into the area left unoccupied by skips. Figure 85 illustrates the upper 2 feet of the root systems of two plants about 17 months old growing in Greenfield loam in the Salinas Valley. The row contained several long skips, and these individuals had no neighbors for a distance of 4 or 5 feet on either side.

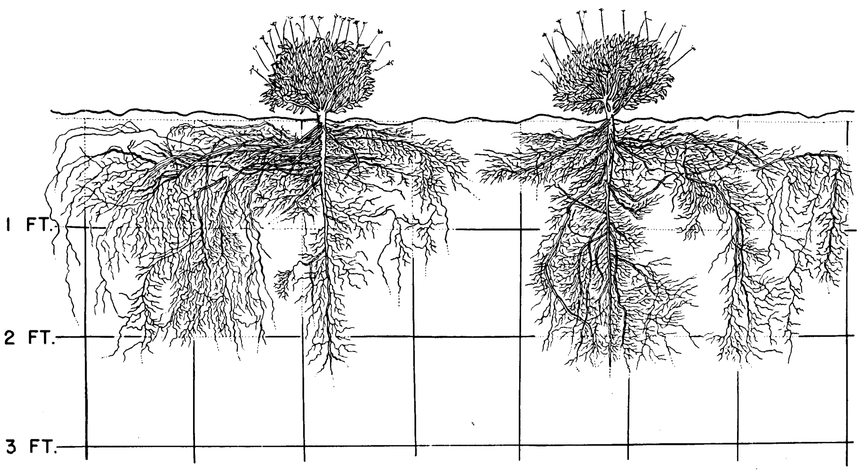

FIGURE 85.—Seventeen-month-old direct-seeded guayule in Greenfield loam in the Salinas Valley, Calif., lacking neighbors on both sides. Only the upper 2 feet of the extensive root system is shown. Note the much greater lateral spread into unoccupied soil than between the two plants.

From the incomplete occupation of the soil between them it may be judged that until recently there had been a third plant between them. Note the much greater spread of the roots to the two sides and the abrupt downward turn of those on the right where they began to encounter the lateral roots of a distant neighbor. In the same pit the plants shown in figure 86 were studied. The total absence of competition on the right side had permitted a lateral spread of the roots of about 4.5 feet in that direction. It is significant that the wider the spread the shallower the eventual depth of penetration and the poorer the soil occupation. Figure 17 shows plants from the same excavation which had had close neighbors on all sides and illustrates the strict habit of closely spaced guayule root systems.

ADVANTAGE OF PRIOR OCCUPATION

The tendency of root systems to spread into adjacent unoccupied soil results in a decided disadvantage to any considerably younger plant

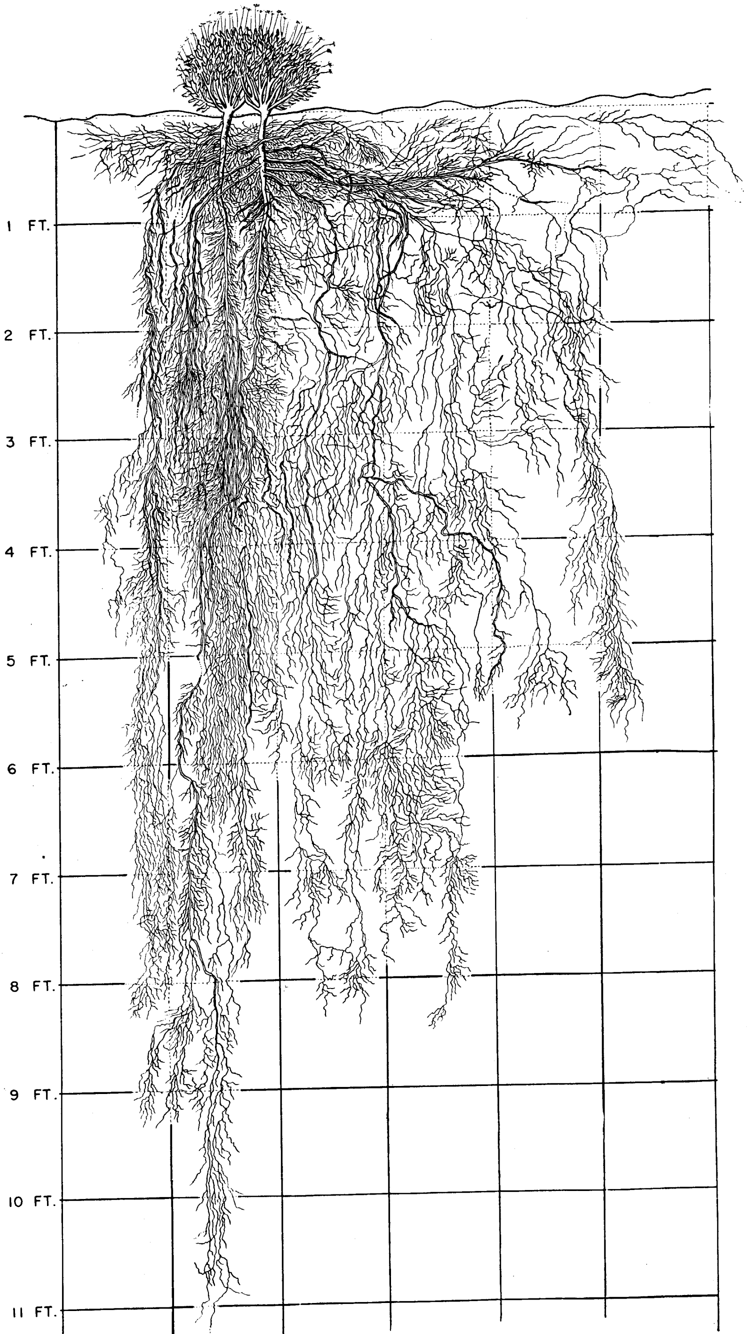

FIGURE 86.—Seventeen-month-old plants adjacent to those shown in figure 85, lacking neighbors on the right but closely crowded on the left. Note the great lateral spread into unoccupied soil and the decrease of penetration with increase of spread.

attempting to accomplish ecesis near a much older one. The previously established roots are ready to absorb any water that might moisten the soil, and the younger plant faces the necessity of growing on a much reduced allotment of water. Figure 87 shows the upper 6 feet of the root systems of three transplants of two ages in Greenfield coarse sandy loam in the Salinas Valley. The plant on the left (*a*) was in the guard row of a planting 9.5 years old. The center (*b*) and right-hand (*c*) individuals were about 3.5 years old. For several years prior to the planting of the center and right-hand rows, the soil to the right of the older plant had been unoccupied and the roots of this plant had spread far to the right. The greater part of the roots beneath the center plant (and even the more prominent roots between the center and right-hand plants) belonged to the old plant on the left. The stunted growth of the center plant, as compared with that of its neighbor of the same age, accurately reflects the depauperate root growth to which it was limited by the advantage of prior occupation possessed by the older plant. That this was no isolated case or mere accident was indicated by the fact that nearly all the plants in the center row were much stunted, most of them being considerably smaller than the one illustrated. Only an occasional individual opposite an extended skip in the row of old plants approached the size of its normal neighbor on the right.

The result of this same principle is often observed in cases of attempted

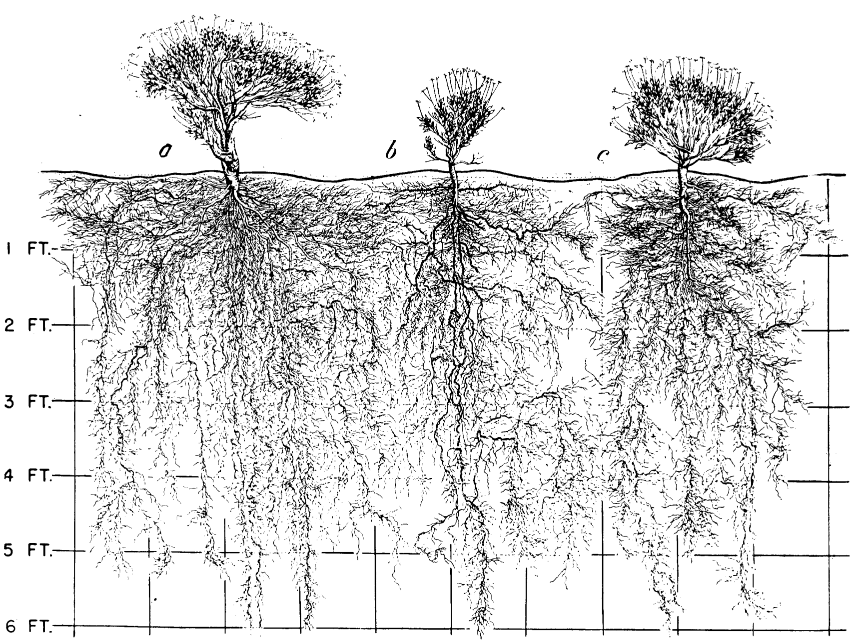

FIGURE 87.—Guayule transplants of two ages in Greenfield coarse sandy loam in the Salinas Valley, Calif.: *a*, 9.5-year-old plant occupying the border row of its plot; *b* and *c*, 3.5-year-old plants. Only the upper 6 feet of the very extensive root systems is shown for *a* and *c*, but the full extent of *b* is included. Note that the roots of the older plant (*a*) had preempted the previously unoccupied space beneath the stunted center plant (*b*) and reached even 2 feet beyond.

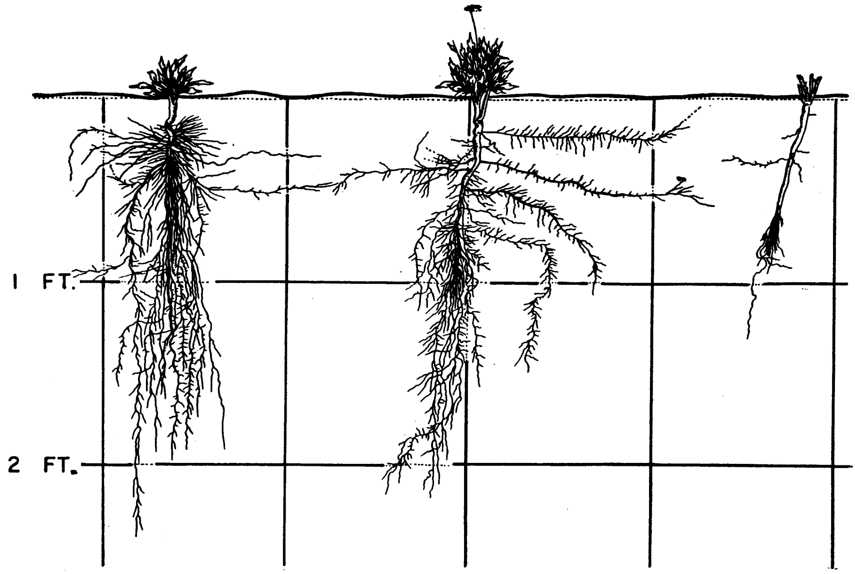

FIGURE 88.—Guayule transplants after 6 months in Lewisville silty clay at San Antonio, Tex., without irrigation. The delayed resumption of growth by the plant on the right is related to early lack of moisture.

interplanting after an original planting has made considerable growth. The late comer not only is never quite able to catch up with the older plants but is retarded by the crowding of roots from adjacent plants enjoying the advantage of prior occupation. This often occurs even without late interplanting. If the nursery stock used in transplanting is not uniformly well hardened off or otherwise physiologically conditioned for immediate growth, a very irregular rate of recovery or sprouting results. This is clearly illustrated in figure 88 which shows plants excavated about the middle of April 1944 at San Antonio. This planting had been put in the previous November and made very little growth before going into winter dormancy. Note that the plant on the right had just begun to sprout, while the others had been actively growing for over a month, having first sprouted the previous fall. Even greater differences result from tardy sprouting of spring- or summer-planted stock. Excessive irregularity of this kind is essentially equal to a poor stand.

EFFECT OF COMPETITION ON YIELD

The relation between spacing and shrub tonnage is a purely agronomic problem and beyond the scope of this paper. However, insofar as spacing is a determinant of competition, its effect upon yield is an ecological principle and the role of root habit in this problem is an important one.

In general, guayule is characterized by a rather extensive root system compared with its aerial size, but the ratio is by no means constant. This relation would indicate that competition for soil space and materials comes into play before above-ground competition. In any ordinary soil, therefore, its volume and the amounts of included nutrients and moisture are apt to become limiting factors in growth before crowding of aerial

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plant parts. Production of maximum plant material on any given site depends upon the full utilization of that required substance that is present in smallest relative amount. Until the available soil volume has been fully occupied by roots, therefore, maximum utilization of the site has not been accomplished.

Excavations of guayule root systems in plots planted with various spacings in several widely separated localities yielded very similar results throughout. Just as nursery plants grown at various stand densities (figs. 82, 83, and 84) in all cases occupied the available soil volume to a similar, rather full degree, in 2-year-old field plantings there was little perceptible difference in the densities of feeder-root concentrations between plants of 12- and 24-inch spacings. Roots of the plants illustrated in figure 74, although spaced at 24 inches, occupied the soil nearly as completely as the adjacent ones illustrated in figure 15, spaced at 12 inches. Similarly, the soil beneath the plants shown in figure 58, spaced at 24 inches, is as fully occupied as that beneath their more closely spaced neighbors illustrated in figure 16.

Greater spacing differentials, on the other hand, especially in younger plants, show widely variable degrees of soil occupation. As shown in figure 86 wide lateral spread was attended by shallower penetration of the spreading roots and poorer soil occupation. Figure 17 illustrates 17-month-old plants spaced an average of 10 inches apart in 28-inch rows in Greenfield loam in the Salinas Valley. In figure 96 (p. 110) are shown 13-month-old plants spaced 48 inches apart in 48-inch rows at a nearby similar site. Both plantings were grown under irrigation. In comparing the root development of the plants illustrated in figures 17 and 96, it is obvious that the soil is not nearly so well occupied under the widely spaced plants as it is beneath the denser stand.

Table 2 shows that at the end of three growing seasons shrubs spaced at 12 inches weighed approximately two-thirds as much as those spaced at 24 inches; yet the greater number of plants resulted in a perceptibly greater tonnage per acre than that produced by the more widely spaced plants. Although competition stunted the closer spaced plants, it resulted in a more complete utilization of the available required materials.

TABLE 2.—*Yields of variously spaced guayule plants, grown from March 30, 1942, to November 15, 1944, Salinas Valley*[1]

Spacing	Plants per acre	Mean shrub weight		Weight of shrub per acre	
		Irrigated	Unirrigated	Irrigated	Unirrigated
	Number	*Ounces*	*Ounces*	*Pounds*	*Pounds*
28 by 12 inches	18,669	8.96	7.26	10,454	8,468
28 by 24 inches	9,334	12.88	8.46	7,513	4,935
28 by 30 inches	7,467	13.50	10.60	6,300	4,946

[1] Data furnished by H. W. Reynolds, Special Guayule Research Project.

Perceptibly full occupation of soil by roots, then, does not necessarily imply full utilization of soil resources. Such utilization arises from keen competition for required soil materials. It may be significant that this coincides also with a somewhat more complete utilization of above-ground resources, such as space. Full utilization of soil volume involves a time element in that plants of a certain spacing will not compete keenly for soil space until age and corresponding size so determine.

Regeneration

In the present method of commercial guayule culture the practice of transplanting involves the removal of the greater part of both the tops and the roots of nursery stock before it is set out. In addition to the chronological study of transplant growth and the excavation of transplanted rooted stem cuttings described previously, attention was paid to many phases of regeneration exhibited by the plant under cultivation.

REGENERATION AFTER TRANSPLANTING

If the plants shown in figure 76 were to be prepared for transplanting, they would be mowed about 1 inch above the surface of the ground and undercut by the passage of a blade through the soil about 6 inches beneath the surface. The resulting 7-inch plant is all of an individual originally 5 or more feet in total length that is transplanted. Considerable regeneration is required before such a plant regains even its former size. That it does so quite rapidly may be seen in the plants illustrated in figure 89, excavated November 17, 1943, at the age of about 14 weeks. The three plants on the right were transplanted, and the two groups on the left are seedlings planted at the same time as the transplants. This excavation was made in an experiment [12] in Greenfield loam in the Salinas Valley.

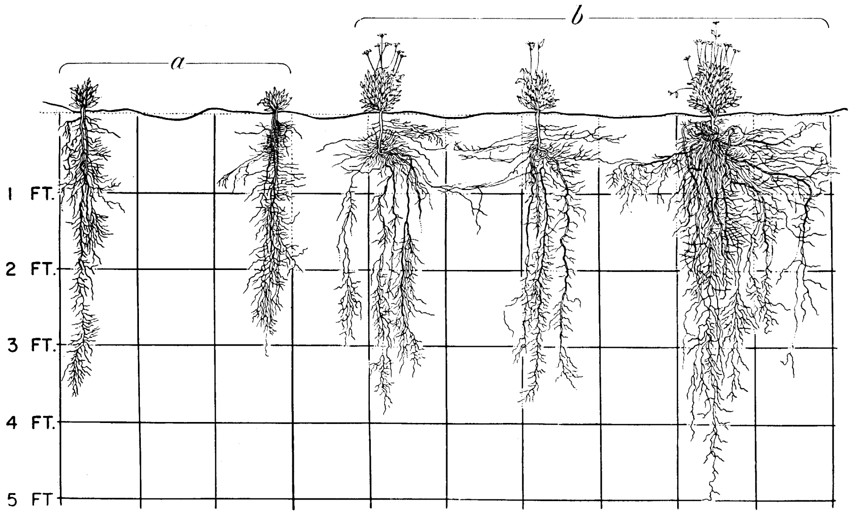

Figure 89.—Fourteen-week-old guayule plants grown in the Salinas Valley, Calif.: *a*, Seedlings thinned to 2 or 3 in a bunch; *b*, transplants.

At an adjacent similar site on Greenfield sandy loam another experiment [12] was undertaken to determine the effect of degree of root pruning on growth. A number of plants were cut to root lengths between 3 and 4 inches (fig. 90) and between 7 and 8 inches (fig. 91). The roots of these plants were studied November 19, 1943, when the plots were about 10 weeks old. No great difference was to be seen between the two classes at

[12] Designed by D. C. Tingey, Special Guayule Research Project.

this stage. If the planting is amply irrigated, it would be expected that only much more drastic pruning would produce a difference. If drying of the surface soil occurs, however, the shorter root stands a greater chance of being desiccated before growth can be resumed and more moist soil depths reached.

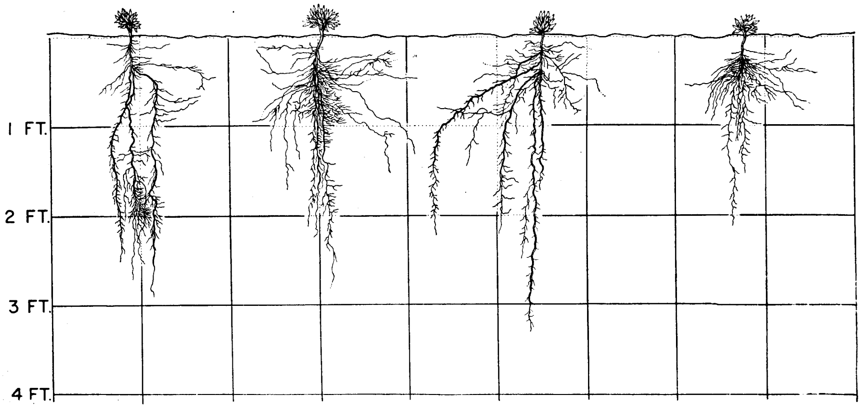

FIGURE 90.—Guayule transplants with roots pruned to between 3 and 4 inches before being planted and grown for 10 weeks in the Salinas Valley, Calif.

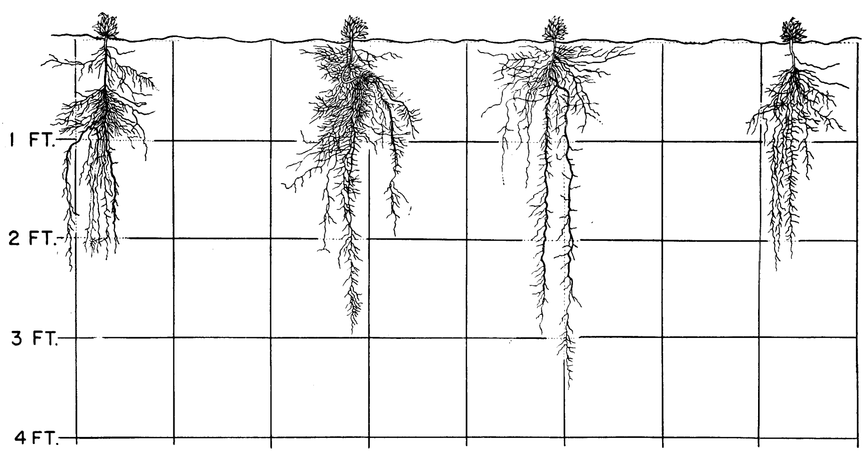

FIGURE 91.—Guayule transplants with roots pruned to between 7 and 8 inches before being planted and grown for 10 weeks, adjacent to those illustrated in figure 90.

REGENERATION BY ROOT SPROUTS, OR RETOÑOS

Root sprouting, or retoño production, of two kinds occurs in guayule. In one leaf buds appear adventitiously upon exposed lateral roots still attached to the living plant. In the other adventitious leaf buds are produced by the exposed ends of residual roots broken from the plant during harvest. Either sort is capable of growing to maturity. The process of retoño production is discussed in detail on page 12.

Figure 92 shows two root sprouts consisting of the budding exposed ends of lateral roots broken from a plant in the process of harvesting.

The plant was pulled in February 1944 from the 2-year-old planting at San Antonio, and the sprouts were excavated about 2 months later. Except for a displacement of some of the branch roots at the upper ends of the roots, there was no disturbance of the root pattern. Such sprouts have a decided advantage in the form of a ready-made root system.

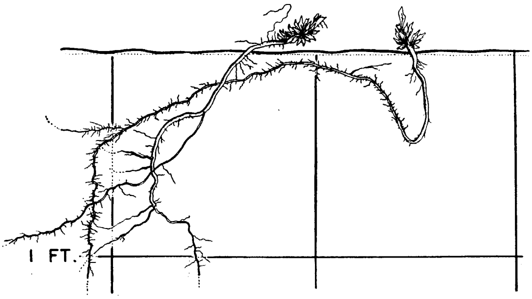

FIGURE 92.—Root sprouts on the residual lateral roots of a 2-year-old guayule plant harvested 2 months earlier from unirrigated Lewisville silty clay at San Antonio, Tex.

A similar but highly artificial form of root sprouting occurred in an old pit that had been dug for the excavation of root systems of 14-year-old guayule and left open for the purpose of observing root sprouting. On the faces of the pit walls were exposed numerous roots of all sizes at depths ranging from a few inches to 15 feet. In some cases these were not attached to plants, the plants having been removed after the study of their root development; others were attached to plants from which a large percentage of the branches had been broken (fig. 93); and still others were attached to quite normal plants. The pit was dug about December 1, 1943, and observations were made on June 23, 1944. In the interim of nearly 7 months a great many root sprouts had appeared, probably in late spring when the moisture of winter precipitation still persisted and the higher temperatures were favorable for growth.

None of the normal plants produced any sprouts on their variously exposed roots, and the two badly broken individuals each produced one root sprout. Of the numerous severed principal roots left by the removal of two plants, about 35 percent sprouted. The tendency to sprout seemed to be inhibited by the presence of a full top, favored by the reduction of the top, and definitely stimulated by severance of the top, indicating that a low top-root ratio was an initiating influence in the sprouting of exposed roots.

Figure 93 shows a severely reduced parent plant with a broken lateral root exposed by the excavation of the pit. The sprouts produced on this root appear in the drawing as though growing beneath the soil, but they actually were growing in the air on the face of the pit wall below the soil level. The distal end of the lateral root was cut and had rotted back to its present length, and the retoños were receiving their water from the intact roots of the parent plant. In other words, the usual direction of water movement in the lateral root had been reversed. This agrees with the result of a reputed incident in the planting of guayule elsewhere. A laborer inserted the wrong ends of the planting stock in the fingers of the planting machine so that the plants were placed in the ground in

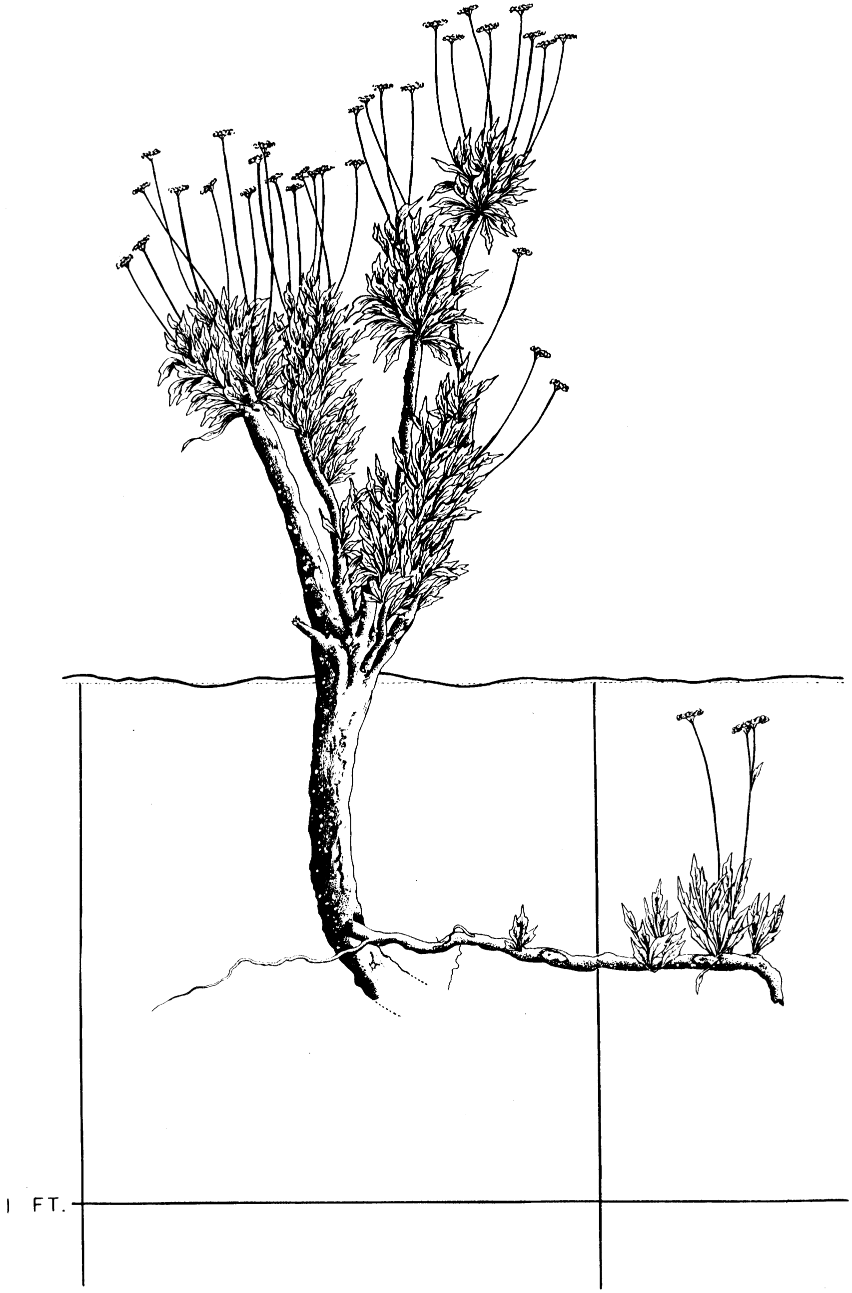

FIGURE 93.—Root sprouts on an exposed lateral root from a broken 14-year-old guayule plant in unirrigated Greenfield coarse sandy loam in the Salinas Valley, Calif. The exposed root protruded from the side of a pit left open over the winter and spring.

an inverted position. When this was discovered several weeks later the plants had sprouted, adventitious leaf buds were appearing on the exposed taproot, and roots were issuing from the buried crown. Polarity seems to be as easily reversed as is the direction of water movement in the xylem.

Figure 94 illustrates various examples of root sprouts on several residual roots on the face of the pit wall at depths ranging from 10 to 52 inches below the soil surface. Apparently lack of sunlight at greater depths limited the production of deeper sprouts. The sprout illustrated in figure 94, *D*, issued from the broken distal end of a secondary branch root. Its connection with the soil was through the still buried distal portion of the principal root to which it was attached. Here, again, the direction of water movement in the branch root had been reversed.

Natural root sprouts, or those issuing from roots still attached to the living mother plant, occur rarely if at all in cultivated guayule on level land, for the stable soil in which it grows minimizes the likelihood of roots being exposed except by destruction of the plant.

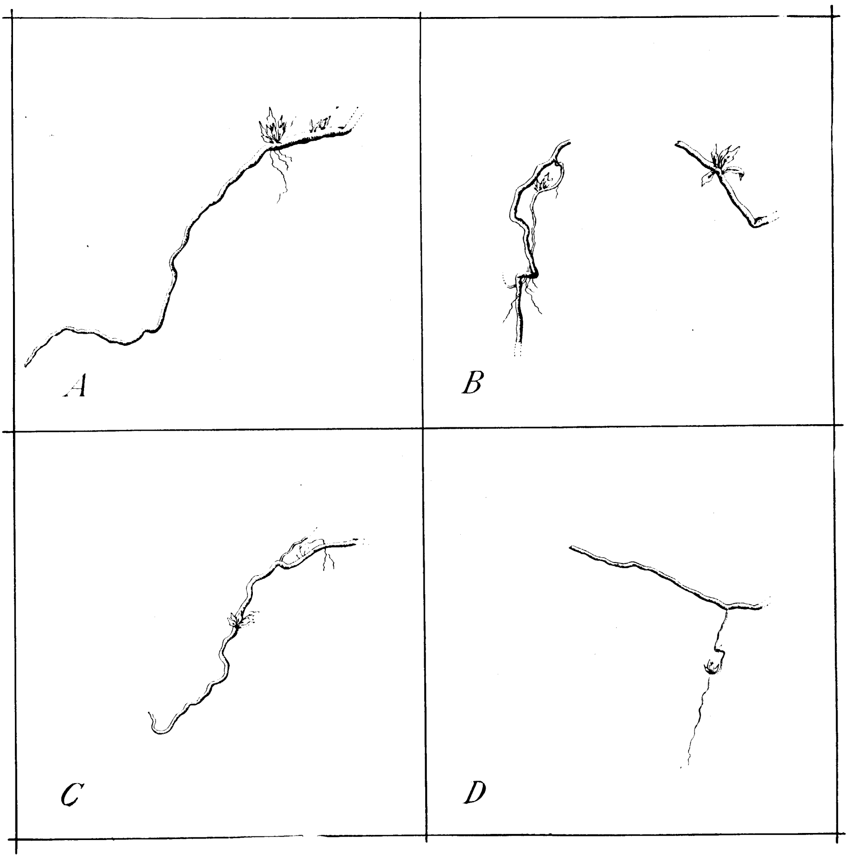

FIGURE 94.—Root sprouts from residual roots left on the wall of an open pit after the guayule plants had been removed. (See fig. 93.) The roots issued from the soil at depths ranging from 10 to 52 inches.

The general capacity of guayule for regeneration is high. The readiness with which it responds to removal of aerial plant parts suggests the practicability of regeneration of an acceptable stand after harvest by mowing. This response is closely akin to the top-root ratio of the residual plant parts. A large body of roots lacking adequate aerial parts seems to stimulate top regeneration markedly. However, the disposition of the present strains of cultivated guayule to contract fatal diseases upon pollarding reduces the hope of mowing as a practical harvesting method.

COMPARISON OF MARIOLA AND GUAYULE UNDER CULTIVATION

The strikingly close resemblance between mariola and guayule in the wild is equally evident when the two are cultivated together. Both show much greater differences in response to habitat than those between the species. Markedly increased vigor and rate of development characterize both under cultivation.

In some genetic studies [13] mariola and guayule were planted adjacent to each other in a deep phase of Greenfield fine gravelly loam in the Salinas Valley in June 1943. The mariola was grown from seed collected in 1942 from the 02 Ranch locality described previously. The guayule was essentially identical with the strain used in the studies of cultivated guayule throughout this work. The plants were spaced 4 feet apart in 4-foot rows, a much wider spacing than ordinarily used in field plantings. The field was irrigated as required to keep the plants active throughout the growing season. The root excavations were made during July 1944, when the plants were 13 months old.

Figure 95 illustrates two mariola plants showing the great vigor of both top and root growth, the relatively efficient and early occupation of a large soil volume, and the abundant tillering of these young plants. Compare with them the two guayule plants illustrated in figure 96, showing the slow top growth of the guayule, the relatively poor soil occupation between the two plants, and the lack of tillering. Compared with the native plants illustrated in figures 9 and 11, however, both species under cultivation show much greater depth of root penetration in the deep, penetrable, moist soil of the field and considerably less tendency of the principal roots to spread laterally.

The cultivation of hybrids derived from guayule and mariola would present no agronomic problems resulting from differences in root habit not encountered in the existing culture of pure guayule. If the tillering habit of mariola were preserved in the hybrids, moreover, greater tenacity of life and maintenance of more nearly perfect stands, even with the practice of harvesting by mowing, would be the expected results.

SUMMARY

Guayule differs from more familiar field crops in having some of the attributes of a desert species. However, it is not truly a desert species, for it requires mesic conditions for active growth. In its native habitat it is characteristic of the class of plants termed drought enduring by Shantz (*14*)—plants that grow when favorable conditions present the opportunity but endure the rigorous conditions of drought in a state of

[13] Designed by LeRoy Powers, Special Guayule Research Project.

inactivity. It is this ability to endure drought that constitutes the most significant practical difference between guayule and other field crops.

Native guayule in trans-Pecos Texas differs from the cultivated plant in two important particulars, both of which relate to the more rigorous habitat. The very shallow water penetration and the imperviousness of

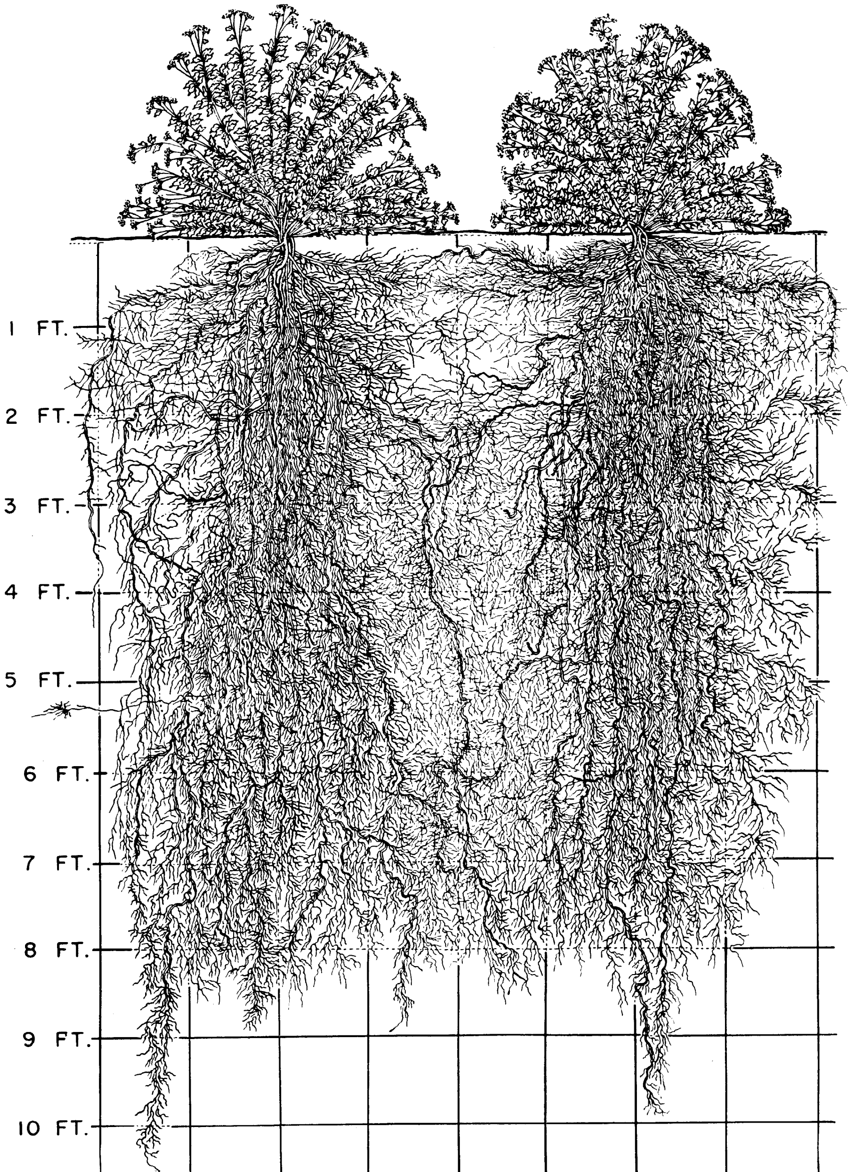

FIGURE 95.—Thirteen-month-old mariola transplants grown under irrigation in Greenfield fine gravelly loam in the Salinas Valley, Calif.

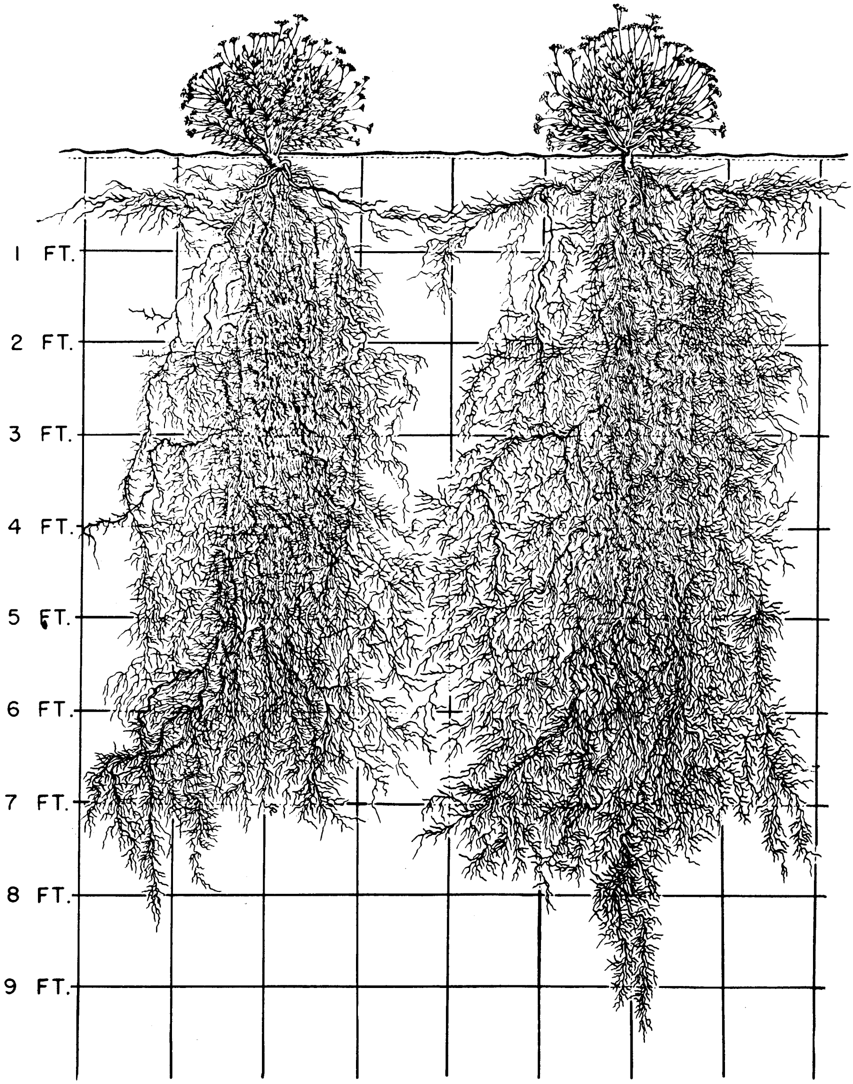

FIGURE 96.—Thirteen-month-old guayule transplants grown under irrigation, immediately adjacent to the mariola plants shown in figure 95.

the hardpan that characterize the native site result in a very shallow and widely extended root system. Mature plants exhibited maximum root depths of 2 to 2.5 feet with lateral spreads up to 10 feet or more. Rate of growth is much reduced by the long periods of desiccation to which the plants are subjected. Seedlings 7 or 8 months old, still exhibiting the taproot habit, had reached depths of 6 or 7 inches and corresponded in development to 19-day-old cultivated seedlings grown under irrigation in the Salinas Valley. In the native habitat conditions are favorable for vigorous growth of guayule a month or two out of the year or rarely longer. Toward the end of a protracted period of drought, the entire soil profile was found to be powder-dry and dusty and the plants had long been dormant. Age determinations based on ring counts revealed 20 years to be the average age of plants corresponding in size to 2-year-old cultivated plants. The species is unable to survive the rigors of a truly desert habitat. Native mariola exhibits a root habit closely paralleling that of native guayule, differing principally in the production of numerous rooted tillers at soil level.

Competition is an important factor in the growth and distribution of native guayule. The species is incapable of withstanding severe competition by fibrous-rooted plants, particularly by grasses and *Agave lecheguilla*. Such competitors deplete the moisture in the shallow horizons occupied by guayule roots before it can be utilized in the reactivation of the guayule plant. Consequently, the species is limited in its natural distribution to a narrow zone altitudinally above the rigorous desert and below the level of grassland development. The most favorable sites are limestone slopes too rocky for the growth of a grass sod. The persistence of native guayule in any given site depends upon its ability to reproduce itself by seedlings and root sprouts, or retoños, after harvest and its protection from browsing by sheep and goats. Browsing by cattle reduces its rate of growth but does not affect reproduction. Overbrowsing by sheep and goats has been observed to bring vigorous stands to the verge of extermination.

In a deep, favorable soil guayule under cultivation is characterized by a modified taproot system. The primary root early loses its dominance, and the system becomes nearly fibrous, consisting of many deep principal roots bearing a dense set of feeder branches. This type of root development is manifested early in the life of the plant and is fully expressed by the end of the second growing season. An isolated plant tends to send its roots out laterally, but under conditions of close spacing there is little lateral spread and little overlapping.

In the guayule seedling the primary root remains dominant, unless its growing tip is killed, for several weeks. By the time the seedling is 2 months old the gradual development of principal lateral roots adumbrates the ultimate fibrous habit. By this time, also, the soil occupation is sufficient to indicate that the seedling is fairly well established so that drought or weed competition would not be fatal. Root depth at this age, though variable, would normally be 2 or 3 feet. Transplants differ from seedlings in the more rapid lateral spread of their roots, while their growth in depth is not noticeably different from that of seedlings. The more rapid occupation of the soil volume by the roots of transplants permits a comparably more rapid establishment of the plants, and they are consequently more quickly prepared to endure drought and competition than are seedlings.

The development of transplanted rooted stem cuttings does not differ from that of ordinary transplanted nursery stock; nor does the development of nursery seedlings differ from that of seedlings in the field.

Soil factors are by far the most effective agents in molding the root habit of guayule under cultivation. Soil texture influences water-holding capacity, aeration, and penetrability to roots. Dune sand was observed to be very unfavorable to root development, probably because of its low water-holding capacity and sterility, while included clay veins encouraged rapid and extensive branching. Dense claypans, on the other hand, because of their slow penetration by both water and roots, resulted in waterlogging and drowning and in severe restriction of root growth. Either form of interference with root development resulted in stunting of the aerial plant parts.

A more severe stunting resulted from the restriction of roots by the formation of a compaction layer in the surface foot of soil resulting from loss of structure through puddling or disturbance while wet. This phenomenon was encountered only in the Salinas Valley, where it is fairly extensive. The effectiveness of the resulting hard layer in stopping root growth depends upon failure of the roots to reach depths in excess of 1 foot before the soil hardens. Therefore, any factor that retards penetration, such as low temperature or loss of the growing root tip by disease, would favor restriction of the roots by the hard layer in any of the several soils predisposed to its formation.

Guayule roots are capable of enduring long periods of desiccation without extensive loss. Soils prone to droughtiness in the upper horizons remain occupied by dormant superficial roots capable of resumption of activity when the soil is again moist. Dry subsoil, on the other hand, is not penetrated by roots. In such situations guayule develops a comparatively shallow root system, corresponding strictly to the depth to which the soil is moistened. Frequency of irrigation is not reflected immediately in root development, although the luxuriance of top growth is directly proportional to this factor.

Root development often seems to correspond closely to the distribution of available nutrients. In a situation characterized by variable depths of favorable loam lying on a coarse sand, depth of root penetration paralleled the extent of favorable soil in spite of variations in frequency of irrigation. Top development, again, was proportional to frequency of irrigation regardless of depth of favorable soil, application of fertilizer, or depth of root penetration.

Guayule is a very poor competitor. It is markedly stunted by weed competition, especially in those early stages of its development when it depends upon the upper foot of soil for its moisture supply. Equal-age competition within the species is characterized by equitable division of the soil resources. Widely spaced plants produce spreading root systems that do not overlap extensively, and the spread is directly proportional to the available space. Proximity of plants of unequal age results in distinct advantage to the older individual. In the interim between plantings the older plant spreads into the adjoining unoccupied soil and does not relinquish this advantage of prior occupation upon the subsequent planting of a younger neighbor. The result is a stunting of the younger plant, a consequence that renders interplanting impractical for purposes of improving a poor stand.

Competition for soil volume and resources in an even stand of guayule favors maximum yield of shrub tonnage. Too wide spacing results in uneconomical utilization of the soil.

The general capacity of guayule for regeneration is high, the loss of either aerial or subterranean parts, within reason, being quickly repaired. This suggests the possible use of mowing as a means of harvesting, provided losses from disease can be reduced after mowing.

Under cultivation mariola responds much like guayule, abandoning its broad shallow root habit for the deep habit seen in cultivated guayule. The possible production of a superior hybrid strain would introduce no agronomic problems relating to root habit not now encountered in guayule; and if the tillering habit of mariola were preserved in the hybrids, the maintenance of more nearly perfect stands, even with the practice of harvesting by mowing, would be expected.

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